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TESIS DOCTORAL

PALEOBIOLOGÍA DE LOS ARTRÓPODOS DEL ÁMBAR CRETÁCICO DE EL SOPLAO (CANTABRIA, ESPAÑA)

ARTHROPOD PALEOBIOLOGY OF THE CRETACEOUS AMBER FROM EL SOPLAO (CANTABRIA, SPAIN)

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Octubre de 2012

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Memoria presentada por Ricardo Pérez de la Fuente, dirigida por Xavier Delclòs Martínez (UB) y Enrique Peñalver Mollá (IGME), para optar al grado de Doctor en Geología. Esta memoria se ha llevado a cabo dentro del programa con mención de calidad de "Ciències de la Terra" de la Universitat de Barcelona y en el marco de los proyectos AMBARES CGL2008-00550 y CGL2011-23948 del Ministerio de Ciencia e Innovación, primero, y de Economía y Competitividad, después (IP: Xavier Delclòs). El periodo de Tesis ha sido financiado directamente durante cuatro años por una beca "Ajuts pel Personal Investigador en Formació" (APIF) de la Universitat de Barcelona. Además, se ha obtenido financiación de la Fundació Agustí Pedro i Pons y los proyectos de la European Synchrotron Radiation Facility (Grenoble, Francia) EC-703 y EC-938. El candidato forma parte del Grup de Recerca Consolidat "Geologia Sedimentària", 2005SGR-00890 (IP: Albert Permanyer) y 2009SGR-01451 (IP: Ramón Salas).

RICARDO PÉREZ DE LA FUENTE

Barcelona, octubre de 2012

EL ÁRBOL DE LA VIDA ~ THE TREE OF LIFE

SI RESPIRO Y SOY,
SI YO SIENTO Y CREZCO,
A MI AIRE, MI SUELO
Y LUZ SE LO DEBO.

I BREATHE AND I AM,
I FEEL AND I GROW,
IN VIRTUE OF MY AIR,
MY LIGHT AND MY SOIL.

QUERRÉ SIEMPRE SER,
DIGAMOS, TU CIELO.
MAS SÓLO SI HACEMOS
JUNTOS LOS LUCEROS.

I WILL ALWAYS WANT
TO BE, SAY, YOUR SKY.
BUT ONLY IF WE DO
THE STARS HAND IN HAND.

Agradecimientos

En contra de la voluntad propia, y para bien o para mal, parece como si lo que uno llegara torpemente a manifestar en este prefacio tuviera la propiedad de permanecer tatuado en el devenir del tiempo, de fosilizar en aquellas retinas que resultan menos extrañas. Cabría, pues, esperar por parte de un esforzado escritor en funciones un cierto anhelo de acariciar, aún con la yema de los dedos, aquella legendaria sabiduría que convierte en granito las palabras y las hace retumbar solemnemente en el eco de los lustros. Pese a ello, pretensiones y aires de grandeza aparte, tan sólo se aprovecharará aquí, desesperadamente y con más pena que gloria, una de las escasas y fugaces ocasiones en las que, a nivel formal y explícito, se permite al científico de a pie sedar a su vertiente autómata y degustar la ambrosía de expresarse con el uso de órganos no cognitivos.

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~

Y aquí estás de nuevo, al fin, como siempre, sonriéndome. Mentar ahora tu nombre sería tan sólo un artificioso modo de pretender dar trascendencia a este momento, cuando de hecho, para mí, tú eres lo que se mantiene y ha de mantenerse trascendente con independencia de la circunstancia y el paso del tiempo. Dedicarte, de algún modo, todo este cúmulo de letras sería, como poco, indecoroso teniendo en cuenta que tú me dedicas algo irrepetible, una parte esencial de tu vida: tus esfuerzos, cuidados y, ante todo, ilusiones.

Tú das sentido a todo esto. Eso va más allá de la gratitud: lo es todo.

And here you are again, in the end, as always, smiling at me. To mention your name now would just be a contrived way of pretending to give significance to this moment, whereas actually, to me, you are what remains and has to remain significant regardless of the circumstance and the passing of time. To dedicate you, somehow, all this heap of letters would be, at the very least, indecorous considering that you dedicate something unrepeatable to me, an essential part of your life: your efforts, care and, above all, illusions.

You give meaning to all of this. That goes beyond gratitude: it is everything.

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1. INTRODUCCIÓN

1.1. Características del ámbar

El ámbar es una resina fosilizada. Pese a sus limitaciones, el ámbar es el material contenedor de fósiles que preserva con mayor detalle organismos del pasado, o partes de los mismos, con una estabilidad medida en millones de años, en contraste con el hielo o la brea, que también son unas materias de conservación muy excepcional aunque mucho menos estables (Martin, 1999). Los fósiles en el interior del ámbar se denominan bioinclusiones. Aun así, lo que convierte el registro de ámbar en excepcional es la capacidad que la resina tuvo de capturar y preservar las paleobiocenosis de un modo relativamente rápido y poco alterado, hecho que confiere al ámbar el potencial de contener evidencias directas de tipo paleoetológico o interacciones paleobióticas.

La resina es una mezcla liposoluble de terpenoides volátiles y no volátiles y/o compuestos fenólicos secundarios que se secreta por estructuras especializadas en la planta (Langenheim, 2003). El significado ecológico de la secreción de resina por parte de las plantas es diverso, aunque su función protectora parece la predominante, bien como mecanismo de cicatrización en reacción a daños causados por factores abióticos (tempestades, fuegos naturales, etc.), como sistema tampón contra la desecación y el cambio de temperatura, o como mecanismo defensivo contra los daños provocados por ataques de hongos o de fitófagos (véase Langenheim, 2003; Martínez-Delclòs et al., 2004). Otras funciones son las de almacenamiento de productos del metabolismo secundario o la atracción de insectos polinizadores (ibid.). Las resinas que dieron lugar al ámbar tuvieron como fuente diversas plantas espermatofitas, tanto gimnospermas (coníferas) como angiospermas; existen grandes depósitos de ámbar del Cenozoico originado a partir de resina de angiospermas (Langenheim, 2003; Grimaldi & Engel, 2005).

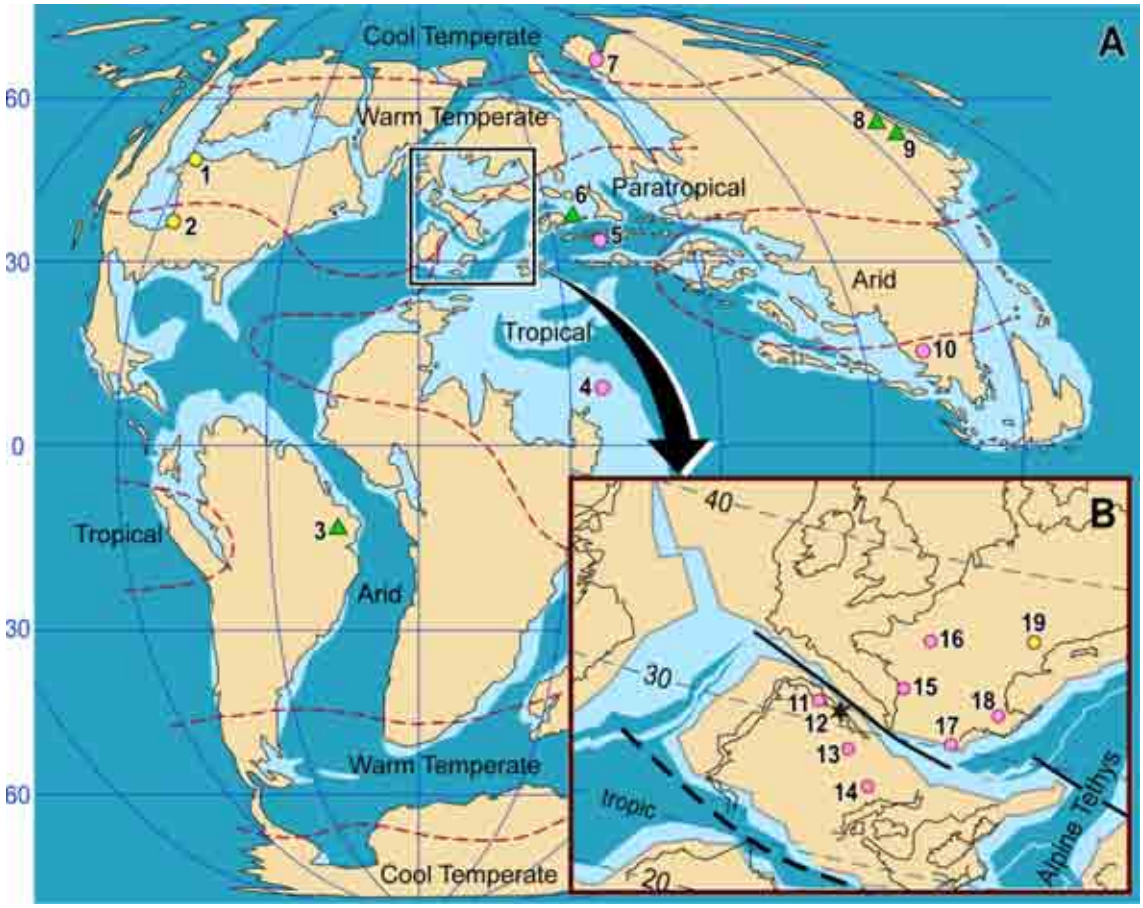
1.2. El ámbar en el Mundo

Pese a que las primeras resinas fósiles datan del Carbonífero (van Bergen et al., 1995; Bray & Anderson, 2009), no existe registro paleobiológico en éstas hasta el Triásico Superior de Italia y Alemania, principalmente microbioinclusiones tales como bacterias, hongos, algas y protozoos (Schönborn et al., 1999; Schmidt et al., 2006). Recientemente se han descrito los primeros artrópodos del ámbar del Triásico de Italia, aunque las macrobioinclusiones que este ámbar ha brindado son escasas (Schmidt et al., 2012).

No existe registro de ámbar con contenido rico en macrobioinclusiones hasta el Cretácico Inferior (Brasier et al., 2009; Azar et al., 2010a; Peñalver & Delclòs, 2010), tratándose principalmente de artrópodos, en su mayoría insectos. Es en esta época cuando la fragmentación de Pangea se incrementa, y asociado a ello tienen lugar alteraciones en las corrientes marinas y ciertas peculiaridades atmosféricas, como una alta concentración de carbono atmosférico y la alteración del régimen de vientos, condicionado por las elevadas temperatura y humedad media (véase Hay, 2008). Ello pudo promover la secreción de grandes

cantidades de resina o la aparición de tal capacidad en ciertos grupos de coníferas (Martínez-Delclòs et al., 2004). También durante el Cretácico Inferior empezaron a diversificarse las angiospermas, lo cual supuso una profunda restructuración y diversificación adaptativa del resto de la biota terrestre (Behrensmeyer et al., 1992; Grimaldi, 1999; Friis et al., 2011).

A nivel mundial, los yacimientos de ámbar del Cretácico son muy escasos, y aquellos con una especial importancia paleontológica, por su diversidad y abundancia en bioinclusiones



▲ **Fig. 1. A**. Yacimientos de ámbar descritos del Aptiense al Cenomaniense. Los yacimientos cuyo ámbar contiene bioinclusiones se simbolizan con un círculo, de lo contrario se usa un triángulo verde. Además, aquéllos ámbares con microorganismos como únicas bioinclusiones (bacterias, protistas, algas y/o hongos) se marcan en amarillo, mientras que los que contienen macrobioinclusiones (fundamentalmente artrópodos) constan en rosa, salvo el ámbar de El Soplao, marcado como una estrella negra. (1) Ruby Creek (Alberta, Canadá); (2) Ellsworth (Kansas, EUA); (3) Nova Olinda-Santana (Ceará, Brasil); (4) Oriente Medio: Wadi Zerka (Amman, Jordania), Bcharreh, Hammana, y Jezzine, entre otros (Líbano), Mt. Hermon (Distrito Norte, Israel); (5) Yukhary Agdzhakend (Goranboy, Azerbaiyán); Federación de Rusia: (6) Stary Oskol (Belgorod), (7) Península de Taimyr (Norte de Siberia), Bahía de Baikura-Neru en el Lago Taimyr (Taimyr Central), Río Nizhnyaya Agapa (Taimyr Occidental), Begichev Fm. en el Río Khatanga (Taimyr Oriental), (8) Río Khetana en Okhotsk del Sur (Krai de Khabarovsk), (9) Cuenca de Suyfun Coal (Primorie); (10) Valle de Hukawng (Kachin, Myanmar). **B**. Área equivalente al marco de la figura A, correspondiente al SW de Europa. España: (11) El Caleyu y Pola de Siero (Asturias), **(12) El Soplao (Rábago, Cantabria)**, (13) Peñacerrada I (=Moraza, en Burgos), Peñacerrada II y Salinillas de Buradón (en Álava), (14) Arroyo de la Pascueta, La Hoya y San Just (Teruel). Francia: (15) Archingeay-Les Nouillers, La Buzinie, Cadeuil, Fouras, l'Ile d'Aix y Les Renardières (Les Charentes), (16) Ecommoy y Durtal (Sarthe y Maine-et-Loire, respectivamente), (17) Fourtou (L'Aude), (18) Salignac y Sisteron (Alpes-de-Haute-Provence); (19) Schliersee (Baviera, Alemania). Figura publicada en Najarro et al. (2009: fig. 1, anexo I.1), redibujada de Blakey (2011) y con las regiones paleoclimáticas de Scotese (2000).

(principalmente artrópodos) quedan restringidos a los ámbares que se indicarán a continuación. Para el Cretácico Inferior, los ámbares del Líbano (las localidades de Hammana, Jezzine y Bcharreh son las principales; Neocomiense-Aptiense), España (localidades más abajo referidas), Myanmar (ámbar de Hukawng, Albiense Superior-Cenomaniense Inferior) y Francia (ámbar de Archingeay-Les Nouillers, Albiense Superior). Para el Cretácico Superior, los ámbares principales provienen de EUA (varias localidades en Nueva Jersey, Turoniense), Federación de Rusia (ámbar de Nizhnyaya Agapa, Cenomaniense Superior, y ámbar de Yantardakh, Santoniense, ambas localidades en la Península de Taimyr) y Canadá (ámbares de Cedar Lake y Grassy Lake, Campaniense). En la Fig. 1 se muestra un mapa paleobiogeográfico mundial con las localidades de ámbar del Aptiense al Cenomaniense y la biozonación climática correspondiente. Véase la Tabla 1 para un listado de los yacimientos mesozoicos conocidos que han proporcionado ámbar con contenido en macrobioinclusiones.

Los yacimientos de ámbar cenozoico han sido estudiados más exhaustivamente, incluso se han explotado comercialmente. Los principales son los ámbares eocenos del Báltico (Weitschat & Wichard, 2002, 2010), y los ámbares miocenos de República Dominicana y Méjico (Solórzano-Kraemer, 2007, 2010; Penney, 2010). Otros yacimientos relevantes de ámbar cenozoico son los de l'Oise (Francia; Nel et al., 2004a) y Cambay (India, Rust et al. 2010), ambos del Eoceno Inferior.

LOCALIDAD	PAÍS	EDAD	REFERENCIAS
TRIÁSICO			
Cortina, Fm. Heiligkreuz	Italia	Carniense Sup.	Roghi et al., 2006; Schmidt et al., 2006; Schmidt et al., 2012
CRETÁCICO INFERIOR			
Hastings	Inglaterra	Valanginiense Inferior	Brasier et al., 2009
Gröling	Austria	Hauteriviense	Borkent, 1997
Isla de Wight	Inglaterra	Barremiense	Nicholas et al., 1993; Jarzembowski, 1999
Hammana, Jezzine, Bcharreh (entre otros)	**Líbano**	**Neocomiense (Aptiense?)**	**Schlee & Dietrich, 1970; Azar, 2000; Veltz, 2008; Azar et al., 2010a**
Wadi Zerka	Jordania	Neocomiense (Aptiense?)	Bandel et al., 1997; Kaddumi, 2007
Choshi	Japón	Barremiense/Aptiense	Fujiyama, 1994
Peñacerrada I (= Moraza) (Burgos)	**España**	**Albiense**	**Alonso et al., 2000; Peñalver & Delclòs, 2010**
Peñacerrada II, Salinillas de Buradón (Álava)	España	Albiense	Corral et al., 1999; Alonso et al., 2000; Arillo et al., 2008a
San Just, Arroyo de la Pascueta, La Hoya (Teruel)	España	Albiense	Peñalver & Martínez-Delclòs, 2002; Peñalver et al., 2006a; Peñalver et al., 2007; Peñalver & Delclòs, 2010
El Soplao (Cantabria)	**España**	**Albiense**	**Najarro et al., 2009 (anexo I.1); Najarro et al., 2010 (anexo I.2)**
El Caleyu, Pola de Siero (Asturias)	España	Albiense	Arbizu et al., 1999; Peñalver & Arillo, 2007; Peñalver & Delclòs, 2010
Archingeay-Les Nouillers, Cadeuil, Les Renardières	**Francia**	**Albiense Sup.**	**Néraudeau et al., 2002, 2005, 2008; Perrichot, 2005; Perrichot et al., 2007, 2010**
Kachin (Hukawng)	**Myanmar**	**Albiense Sup. -Cenomaniense Inf.**	**Cockerell, 1917; Grimaldi et al., 2002; Cruickshank & Ko, 2003; Ross**

			et al., 2010; Shi et al., 2012
Cuenca del río Khatanga (Taimyr)	Federación de Rusia	Albiense Sup. -Cenomaniense Inf.	Zherikhin & Eskov, 1999; Rasnitsyn & Quicke, 2002
Yukhary Agdzhakend	Azerbaiyán	Albiense Sup. -Cenomaniense Inf.	Zherikhin & Eskov, 1999; Rasnitsyn & Quicke, 2002
CRETÁCICO SUPERIOR			
La Buzinie	Francia	Cenomaniense Inf.	Perrichot et al., 2007
Fourtou	Francia	Cenomaniense Inf.	Perrichot et al., 2007
Île d'Aix, Fouras	Francia	Cenomaniense Inf.	Schlüter, 1978; Néraudeau et al., 2003, 2009
Salignac	Francia	Cenomaniense	Perrichot et al., 2007
Ecommoy, Durtal	Francia	Cenomaniense	Schlüter, 1978; Perrichot, 2005
Alem Ketema	Etiopía	Cenomaniense	Schmidt et al., 2010
Río Nizhnyaya Agapa (Taimyr)	**Federación de Rusia**	**Cenomaniense Sup.**	**Zherikhin & Eskov, 1999; Rasnitsyn & Quicke, 2002**
Timmerdyakh (Yakutia)	Federación de Rusia	Cenomaniense-Turoniense	Zherikhin & Eskov, 1999; Rasnitsyn & Quicke, 2002
Nueva Jersey (varios depósitos)	**EUA**	**Turoniense**	**Wilson et al., 1967; Grimaldi et al., 1989; Grimaldi et al., 2000; Grimaldi & Nascimbene, 2010**
Shavarshavan	Armenia	Coniaciense	Zherikhin & Eskov, 1999; Rasnitsyn & Quicke, 2002
Yantardakh (Taimyr)	**Federación de Rusia**	**Santoniense**	**Zherikhin & Sukatsheva, 1973; Zherikhin & Eskov, 1999; Rasnitsyn & Quicke, 2002**
Fm. Eutaw (Alabama)	EUA	Santoniense	Knight et al., 2010
Kuji	Japón	Santoniense	Schlee, 1990
Piolenc, Belcodène	Francia	Santoniense	Gomez et al., 2003
Grassy Lake (Alberta), Cedar Lake (Manitoba)	**Canadá**	**Campaniense**	**Carpenter et al., 1937; McAlpine & Martin, 1969; Pike, 1995; McKellar et al., 2008; McKellar & Wolfe, 2010**
Bahía de Baikura-Neru (Taimyr)	Federación de Rusia	Cretácico Sup.	Zherikhin & Eskov, 1999; Rasnitsyn & Quicke, 2002

▲ **Tabla 1.** Ámbares mesozoicos con contenido en macrobioinclusiones. Los principales yacimientos en términos de paleobiodiversidad recuperada (con más de 500 bioinclusiones conocidas) se marcan en negrita. Los yacimientos españoles se muestran sombreados.

1.3. El ámbar del Cretácico de España

A pesar de que el primer estudio detallado del ámbar de España data del siglo XVIII, en un tratado de la historia natural y médica del Principado de Asturias (Casal, 1762), y que mucho más tarde Boscá (1910) indicará por vez primera la posible presencia de bioinclusiones, no es hasta el año 1994 con el descubrimiento del ámbar de Álava (yacimientos de Peñacerrada I y II), que el estudio científico del ámbar de España y sus bioinclusiones se inicia. Sin embargo, los otros ámbares cretácicos de relevancia científica procedentes del Líbano, Myanmar, Francia, EUA (Nueva Jersey), Federación de Rusia (Taimyr) y Canadá se estudiaron desde mucho antes (Cockerell, 1917; Carpenter et al., 1937; Wilson et al., 1967; Schlee & Dietrich, 1970; Zherikhin & Sukatsheva, 1973; Schlüter, 1978). Pese a este condicionante, las colecciones de ámbar de España son hoy en día un referente a nivel mundial.

Hasta la fecha, unos 120 yacimientos de ámbar del Cretácico han sido catalogados en España, siendo la mayoría de ellos de edad Albiense (Peñalver & Delclòs, 2010). No obstante, sólo nueve de estos yacimientos han proporcionado ámbar que contenga macrobioinclusiones, principalmente artrópodos (Peñalver & Delclòs, 2010; Fig. 1B). Sólo tres han proporcionado un elevado número de bioinclusiones muy diversas en su conjunto: Peñacerrada I (= Moraza) en Burgos (Alonso et al., 2000), San Just en Teruel (Peñalver et al., 2007), y El Soplao en Cantabria, objeto del presente Proyecto de Tesis Doctoral. El yacimiento de Peñacerrada I, en el burgalés condado de Treviño, ha sido el más extensamente estudiado hasta la fecha. Cuenta con más de 2000 bioinclusiones descubiertas durante estos últimos 17 años, pertenecientes a 16 órdenes de hexápodos, tres órdenes de arácnidos y dos órdenes de crustáceos (Peñalver & Delclòs, 2010). La colección de ejemplares de este ámbar se encuentra depositada en el Museo de Ciencias Naturales de Álava (Vitoria). Por otra parte, el yacimiento de San Just en Teruel, descubierto a finales de los años 90 e investigado desde el año 2003, cuenta actualmente con más de 200 bioinclusiones catalogadas, recuperadas en varias intervenciones. Esta colección se encuentra depositada en la Fundación Conjunto Paleontológico de Teruel-Dinópolis (Teruel). Los seis yacimientos españoles con escaso contenido en macrobioinclusiones corresponden a los de El Caleyu y Pola de Siero en Asturias (Arbizu et al., 1999; Peñalver & Arillo, 2007), Peñacerrada II y Salinillas de Buradón en Álava (Alonso et al., 2000; Arillo et al., 2008a), Arroyo de la Pascueta en Teruel y La Hoya en Castellón (Peñalver & Martínez-Delclòs, 2002; Peñalver et al., 2006a). Los ámbares no cretácicos en la Península Ibérica han aparecido en pequeñas cantidades, hallándose en el Triásico Superior (Keuper) de Alicante, y en los sedimentos lacustres miocenos de Rubielos de Mora en Teruel y Ribesalbes en Castellón (Peñalver & Delclòs, 2010).

El descubrimiento del yacimiento de ámbar de El Soplao (Rábago, Cantabria; Fig. 2) motivó el presente Proyecto de Tesis Doctoral principalmente por dos motivos. Primero, la estratigrafía y sedimentología, así como los aspectos geoquímicos del ámbar y los primeros estudios de macroflora y palinología, fueron tratados con anterioridad a cualquier otro estudio (véase Najarro et al., 2009: anexo I.1). Este hecho posibilitó que desde un inicio se asentaran desde un enfoque pluridisciplinar los resultados del presente Proyecto de Tesis Doctoral. Y segundo, ya desde las primeras campañas de excavación en marzo del 2008, el yacimiento se reveló como excepcionalmente rico tanto en piezas de ámbar (y su proporción de piezas de origen aéreo) como en bioinclusiones.

▲ **Fig. 2.** Vista general del yacimiento de El Soplao, en Rábago (Cantabria). **A**. Aspecto del yacimiento en 2008, antes del inicio de las excavaciones. **B**. Aspecto actual del yacimiento. Fotografías por Xavier Delclòs.

2. OBJETIVOS

2.1. Objetivo principal

La finalidad principal de este Proyecto de Tesis Doctoral ha sido alcanzar un nivel de conocimiento elevado sobre la paleobiología asociada a los artrópodos del yacimiento de ámbar de El Soplao, que permita una primera comparación con los yacimientos principales de ámbar cretácico, tanto españoles como extranjeros. Ello, tras considerar los sesgos tafonómicos existentes, ha supuesto reconocer, describir y determinar taxonómicamente los artrópodos del ámbar de El Soplao, preferentemente aquéllos con un mayor potencial informativo, con el fin de realizar inferencias paleoautoecológicas, paleobiogeográficas y paleoetológicas que permitieran llevar a cabo una reconstrucción paleoambiental lo más fidedigna posible.

2.2. Hipótesis de trabajo

A continuación se listan las hipótesis de trabajo asociadas a los objetivos secundarios que se establecieron desde el inicio de este Proyecto de Tesis Doctoral.

● 1. Hipótesis: La paleobiota de artrópodos de la Península Ibérica presenta endemismos biológicos durante el Cretácico Inferior debido a su aislamiento insular adquirido unos 100 millones de años atrás. Objetivo: Comparación de la paleobiota de El Soplao, conjuntamente con sus análogas cretácicas españolas, con aquéllas del resto del mundo para la detección de discrepancias o peculiaridades paleobiológicas.

● 2. Hipótesis: El estudio de las bioinclusiones de artrópodos (básicamente arañas e insectos), bien sea por sus características paleobiológicas como por sus abundancias relativas, proporciona relevante información paleoecológica y paleoambiental del medio terrestre. Objetivo: Selección de aquellos grupos de artrópodos con mayor potencial informativo desde el punto de vista paleobiológico. Descripciones y determinaciones taxonómicas. Estudios paleoecológicos y filogenéticos.

● 3. Hipótesis: El registro de ciertos grupos de artrópodos incluidos en el ámbar está controlado, además de por otros factores tafonómicos, por factores necrobióticos de tipo paleobiológico (etología, hábitat, morfometría, etc.). Objetivo: Tras la consideración del total de sesgos tafonómicos, deducir algunos aspectos paleoecológicos a partir de la presencia o ausencia de ciertos taxones en el registro.

● 4. Hipótesis: La paleobiota del ámbar de El Soplao refleja un ambiente de formación de las piezas de resina muy próximo al mar, al contrario que otros yacimientos de ámbar españoles, y

ello está en consonancia con los datos estratigráficos y sedimentológicos. Objetivo: Estudio de las bioinclusiones de entidades paleobiológicas que pudieron estar directa o indirectamente vinculadas a un ecosistema especialmente húmedo o de marcada influencia marina, separándolas de las eminentemente terrestres, para su comparación con las aparecidas en otros yacimientos.

● 5. Hipótesis: La elevada acumulación de ámbar en el yacimiento fue en gran medida consecuencia de paleoincendios. Objetivo: Detección de grupos de artrópodos potencialmente relacionados con las primeras etapas regenerativas del bosque de coníferas (como las avispas Anaxyelidae). Estudio de macro- y mesorrestos vegetales, también aquéllos fusinizados, tanto asociados a los ámbares como los existentes en forma de inclusiones en ámbar.

● 6. Hipótesis: En los bosques cretácicos, las arañas desarrollaron diversas estrategias de caza según el subhábitat y la presa, habiendo ya de existir, como en la actualidad, diferentes morfologías de telas. Objetivo: Descripción y determinación taxonómica de los grupos de arañas. Inferencia de su paleoecología. Análisis morfológico de las telas de araña conservadas y determinación de sus implicaciones paleoecológicas.

● 7. Hipótesis: En la asociación fósil contenida en el ámbar de El Soplao se refleja una dominancia de grupos de artrópodos similar a la de los otros yacimientos cretácicos de ámbar. Objetivo: Determinación de la abundancia relativa de los distintos grupos de artrópodos y análisis de su significado paleoecológico y/o tafonómico.

● 8. Hipótesis: La aparición durante el Cretácico Inferior de nuevos grupos de insectos barrenadores de madera, como es el caso de algunos coleópteros, promovió la secreción de resina como mecanismo defensivo en los árboles afectados. Objetivo: Estudio de los insectos que potencialmente tuvieron hábitos destructores de tejido arbóreo, preferentemente aquéllos que constituyan primeras apariciones en el registro fósil.

3. METODOLOGÍA DE TRABAJO

3.1. Trabajo de campo: obtención del ámbar

La obtención de ámbar del yacimiento de El Soplao fue una de las prioridades principales durante los inicios de este Proyecto de Tesis Doctoral, ya que el descubrimiento del yacimiento se produjo en 2007 y, pese a que ya se contaba con una pequeña colección de inclusiones fruto de prospecciones superficiales, fue necesario ampliar el número de bioinclusiones disponibles para estudio. Para tal fin, se realizaron cuatro campañas de excavación en el yacimiento de El Soplao, durante los meses de octubre de 2008, marzo de 2009, julio de 2009 y marzo de 2010. El doctorando participó en las tres primeras.

3.1.1. Zonas de obtención del ámbar

- En superficie. Se recogió material lavado por la lluvia y expuesto en el talud que constituye el yacimiento cuando éste fue descubierto y durante las siguientes prospecciones realizadas.
- Niveles ricos en ámbar. La extracción de ámbar en los niveles se produjo principalmente durante la primera excavación, en octubre de 2008 (Fig. 3A). Se practicó la extracción manual y la extracción por flotación a partir del sedimento retirado (véase el apartado 3.1.2).

▲ **Fig. 3**. Tareas llevadas a cabo sobre el yacimiento de El Soplao. **A.** Trabajos de extracción manual de ámbar durante la excavación de octubre de 2008. **B.** Excavadora realizando la calicata principal donde luego se llevaría a cabo la extracción mediante lavado directo con agua a presión, marzo de 2009. Fotografías: A por Xavier Delclòs; B por Rafael López del Valle.

- Calicata principal. Este fue el lugar principal de extracción durante las excavaciones de 2009 y 2010, y el punto del que se ha extraído una mayor cantidad de ámbar en el yacimiento de El Soplao. Sus dimensiones iniciales aproximadas fueron de 7 x 2,5 x 2 m (longitud/anchura/profundidad) y fue realizada por una pala excavadora (Fig. 3B). En este punto se practicó la extracción mediante lavado directo con agua a presión, por lo

que la calicata ha ido incrementando su amplitud y profundidad (véase el apartado 3.1.2). Tanto el sedimento retirado por la excavadora al realizar la calicata, como el sedimento acumulado en la malla del cuello basal de la calicata (parte más baja de ésta) tras sucesivos lavados con agua a presión se sometieron posteriormente a una criba por flotación

- Calicatas secundarias. Se llevaron a cabo para constatar la continuidad lateral del yacimiento durante la excavación de 2010. Se realizaron dos, una a cada lado de la principal, a una distancia aproximada de unos 10 metros de esta última.

3.1.2. Técnicas de extracción del ámbar

Las tres técnicas que a continuación se exponen son las que se utilizaron para la extracción de piezas de ámbar durante las excavaciones.

- Extracción manual mediante herramientas convencionales (Fig. 4). Para la extracción manual se usaron picos, palas, escalpelos, etc. Este método supone un sesgo hacia piezas de ámbar de tamaño medio-grande y presenta una eficiencia baja respecto a las otras dos técnicas aplicadas. Las superficies de muchas piezas de ámbar, por estar recubiertas de sedimento o por presentar una corteza opaca, carecen de brillo y por tanto son difíciles de identificar a simple vista. Por ello, con este sistema se recuperan principalmente las piezas fragmentadas y por ello brillantes. Esta problemática se reduce de forma significativa en las otras dos técnicas. Durante la extracción de piezas grandes es aconsejable mantener la matriz de sedimento de alrededor para asegurar la integridad de las piezas de ámbar durante su traslado al laboratorio, donde se consolidan si es necesario. Por otra parte, se ha observado que la gran mayoría de las piezas de ámbar de tamaño grande no contienen bioinclusiones, por lo que este método supone un sesgo importante para la obtención de bioinclusiones (véase Pike, 1993)

- Extracción por flotación (Fig. 5). Este método es el más exhaustivo pues recupera todo el rango de tamaños de las piezas de ámbar. Se basa en la propiedad del ámbar de flotar en agua saturada de sedimento en suspensión, ya que la mezcla de agua y sedimento es más densa que el ámbar. El uso de hormigoneras para el lavado de sedimento permite el procesado rápido de mucho material (Corral et al., 1999; Nascimbene & Silverstein, 2000). El movimiento de la hormigonera junto a la acción del agua añadida desmenuza progresivamente el sedimento con ámbar (una matriz arcillosa-arenosa rica en materia orgánica). El ámbar asciende en la mezcla por flotación, junto a otros restos vegetales fósiles como cutículas y trozos de lignito, y se mantiene flotando también debido al movimiento rotatorio continuo. Gracias a esto, las piezas de ámbar se pueden retirar por sucesivos volcados del contenido de la hormigonera sobre tamices de malla fina. Sobre estos tamices se recogen manualmente las piezas de ámbar tras un aclarado con agua limpia. Gracias a todo este proceso las piezas de ámbar quedan limpias de restos de sedimento lo cual facilita

su reconocimiento. La técnica, al contrario de lo que en un principio podría parecer, resulta muy poco agresiva, y se ha llegado a recolectar intactas piezas sumamente delicadas. Se ha calculado que el porcentaje de recuperación de las piezas de ámbar es muy alto, superior al 98%. El valor de este porcentaje se ha obtenido tras revisar el sedimento sobrante de la hormigonera un año después de su primer procesado.

▲ **Fig. 4.** Proceso de extracción de una pieza grande de ámbar de importancia tafonómica, descubierta en la calicata principal del yacimiento de El Soplao, excavación de marzo de 2010. **A**. Pieza tal y como quedó al descubierto tras el lavado directo (flecha). **B.** Inicio de las labores de retirada del sedimento circundante. Tanteo del tamaño de la pieza bordeando su área con la ayuda de un escalpelo. **C.** Retirada de sedimento presente en la parte superior de la pieza y sus bordes. **D.** Aspecto de la muestra tras su lavado *in situ* con agua. Nótese su característico color púrpura. Vista frontal. **E.** Ídem. Vista superior. Nótese el patrón de cicatrices superficiales. **F.** Aspecto de la muestra tras el proceso completo de liberación del sedimento acompañante. Nótese su posición paralela a los planos de estratificación. **G.** Extracción de la pieza.

- Extracción mediante lavado directo con agua a presión (Fig. 6). Es la primera vez que esta técnica se ha puesto en práctica en una excavación de ámbar. Se aplicó durante la

excavación de julio de 2009 (véase Najarro et al., 2010: anexo I.2). Con ella se consigue de forma eficiente dejar al descubierto masas de ámbar de gran tamaño que pueden luego ser extraídas enteras (Fig. 4). El agua a presión se aplicó sobre las paredes verticales de la calicata. El sedimento que se disgregó dejó al descubierto las masas de ámbar de mayor tamaño que posteriormente se pudieron extraer manualmente. Por otra parte, el agua que arrastró el sedimento con trozos pequeños de ámbar se concentró en el cuello de la calicata, al final de su longitud máxima, donde dos mallas de luz decreciente lo retuvieron. Este sedimento se retiró y posteriormente se cribó por flotación usando la hormigonera y el tamiz (véase el punto anterior).

▲ **Fig. 5.** Proceso de extracción de ámbar mediante flotación. **A.** Carga de sedimento y agua en una hormigonera. **B.** Volcado del contenido con ámbar y otros materiales en suspensión sobre el tamiz. **C.** Selección manual de las piezas de ámbar. **D.** Aspecto de algunas de las piezas recogidas. **E.** Separación de piezas recuperadas en contenedores con agua. Nótese el material que permanece en el tamiz, mayoritariamente lignito. Fotografías: A y B por Xavier Delclòs; C, D y E por Rafael López del Valle.

3.2. Trabajo de laboratorio: preparación del ámbar

Una vez el ámbar ha sido obtenido en la excavación, empieza una laboriosa tarea de limpieza de las piezas recuperadas, detección de bioinclusiones, preparación y, finalmente, gestión de la base de datos que registra las bioinclusiones. Todo este trabajo de laboratorio ha sido realizado por el geólogo/gemólogo Sr. Rafael López del Valle, técnico especializado en preparación de ámbar y miembro del equipo AMBARES. La metodología se expone aquí brevemente; para una descripción más detallada véase Corral et al. (1999) y Nascimbene & Silverstein (2000).

▲ **Fig. 6.** Extracción de ámbar mediante lavado directo con agua a presión en el yacimiento de El Soplao, excavación de marzo de 2009. **A.** Chorro de agua a presión aplicado sobre una de las paredes de la calicata principal. **B.** El agua cargada con sedimento drena por gravedad hacia el cuello de la calicata, donde dos mallas en serie (de 1 cm y 1/2 cm de luz, consecutivamente) retienen el sedimento con ámbar. **C.** Detalle de una de las piezas de ámbar *in situ* descubierta tras uno de los lavados. **D.** Aclarado de la primera malla. Nótese la existencia de una segunda malla posterior, de luz inferior, para retener el ámbar de menor tamaño. **E.** Aspecto del sedimento con ámbar en la primera malla tras el aclarado. **F.** Muestra de varios fragmentos de tamaño medio recolectados en la primera malla. Los fragmentos formaban parte de piezas de ámbar de forma arriñonada. Fotografías: A y F por Rafael Lozano; B y E por Xavier Delclòs; C por Rafael López del Valle.

3.2.1. Limpieza y consolidación

Las piezas procedentes del campo son lavadas con agua, preferiblemente destilada, para eliminar los restos de sedimento. Una vez limpias de sedimento, a menudo es necesario recurrir al uso de bisturís, pinceles o incluso una cubeta de ultrasonidos para eliminar el

sedimento más consolidado y adherido, principalmente si la superficie del ámbar presenta fracturas. A menudo es necesario llevar a cabo la consolidación de las piezas de ámbar mediante la aplicación de productos acrílicos en las superficies y grietas con la ayuda de una brocha o una jeringuilla. Este procedimiento es común para aquellas piezas de mayor tamaño, con importancia tafonómica y escasa probabilidad de contener bioinclusiones, a las que no se aplican los siguientes pasos.

3.2.2. Triaje

Cada una de las piezas o fragmentos de ámbar se observa bajo la lupa binocular en busca de bioinclusiones. Hasta la pieza más pequeña de ámbar puede contener bioinclusiones, pues el tamaño medio de las bioinclusiones es de 1-2 mm y se han encontrado ejemplares de insectos con tamaños inferiores a un milímetro. En ocasiones es necesario pulir la superficie de la pieza de ámbar para observar su interior, por ejemplo si presenta una corteza opaca.

3.2.3. Preparación

La preparación debe ser realizada poco tiempo después de extraer las piezas del yacimiento, ya que el ámbar es un material muy lábil, cuya superficie externa se oxida y cuartea con gran facilidad si no es convenientemente tratado y almacenado, peligrando el estado de conservación de las posibles bioinclusiones. La correcta preparación inicial es un aspecto fundamental para garantizar la conservación a largo plazo.

Una vez se han separado aquellas piezas con bioinclusiones, se procede a eliminar la máxima cantidad de ámbar que circunda la bioinclusión o bioinclusiones a estudiar, para mejorar su visibilidad. Para ello se utiliza primero una cortadora circular de precisión y luego una lijadora circular con lijas de granulometría decreciente, las cuales eliminan marcas de sierra e irregularidades.

La preparación de las bioinclusiones en ámbar de España se realiza mediante su inclusión en resina sintética tipo epoxy (EPO-TEK 301), que es termoestable, de baja viscosidad y con un índice de refracción similar al del ámbar (por ello no se producen distorsiones ópticas apreciables). La inclusión en resina epoxy se realiza en una cámara de vacío para conseguir un mayor grado de penetración de la resina por eventuales fracturas. Este aspecto es importante ya que las fracturas reflejan la luz dificultando el estudio. La cámara de vacío está provista de unas varillas longitudinales en donde se deposita la pieza de ámbar a incluir; esta es una modificación de la cámara de vacío de Tucker. Una vez creado el vacío se hacen girar las varillas por lo que el ámbar cae en la resina epoxy mientras se cataliza en unos moldes de silicona o látex. El vacío facilita que el aire del interior de las fracturas del ámbar y de la resina epoxy escape, minimizándose la creación de burbujas. Una vez completado este proceso y antes de que se complete la catálisis, se permite la entrada de aire a la cámara de vacío muy lentamente. En este paso del proceso el ámbar flota en la resina y se ha de orientar con la ayuda de unas agujas. La resina epoxy tarda unas 24 horas en endurecerse a temperatura ambiente.

La preparación resultante se corta y se lija con los métodos expuestos anteriormente para dejar la bioinclusión lo más cerca posible de la(s) superficie(s) de la preparación. El pulido final para proporcionar la máxima transparencia a las superficies de la preparación se realiza manualmente frotando sobre una gamuza con el uso de una pasta de pulido.

Antiguamente se usaban para la conservación de las preparaciones de ámbar algunos productos, como aceites minerales o bálsamo del Canadá disuelto en xileno aplicado al vacío, que se han revelado perjudiciales a largo plazo.

3.2.4. Colecciones, siglas y gestión de la base de datos de la "Colección El Soplao" (CES)

Cada una de las preparaciones fue asignada con una entrada de registro en la base de datos de la "Colección El Soplao" (CES). Este material se halla actualmente depositado en la Colección Institucional del ámbar de El Soplao en la Cueva de El Soplao (Celis, Cantabria). Cada entrada de registro lleva asociada un número de inventario CES único, por ejemplo "CES 530". La colección se compone no sólo de preparaciones con bioinclusiones sino también de piezas de ámbar sin bioinclusiones pero con valor tafonómico o material paleontológico asociado al ámbar del yacimiento de El Soplao. Las diferentes bioinclusiones preservadas conjuntamente en una misma pieza de ámbar, o sininclusiones (Koteja, 1986), comparten ese número de inventario más un número que acompaña, tras un punto, al número de inventario, por ejemplo, "CES 530.7" (preparación número 530, sininclusión número 7; Fig. 7). Además, varias preparaciones pueden proceder de una misma pieza de ámbar originaria aunque hayan sido preparadas independientemente para su cómodo estudio. En tal caso, queda registro de que todas esas inclusiones son sininclusiones en un número independiente llamado "referencia de sininclusión" (= RS). Por ejemplo, las muestras CES 530 (con 24 sininclusiones) y CES 531 comparten el número de referencia de sininclusión "27" y por tanto las inclusiones de ambas muestras son sininclusiones entre sí. Para cada entrada de inventario se hace constar una determinación taxonómica preliminar de cada una de las inclusiones en la preparación, a nivel normalmente de orden si es posible. Luego este campo taxonómico se amplía tras el estudio u observación más detallada por parte de los miembros investigadores del equipo. Asimismo, se hace constar en el campo "estatus" si el ejemplar representa alguno de los ejemplares tipo de una nueva especie o si el ejemplar ha sido figurado en alguna publicación. Todos los campos anteriormente citados se proporcionan en el anexo II. Como añadido, existen otros campos que a nivel técnico se hacen constar en la base de datos CES, como las dimensiones y el peso de la muestra, si se halla en préstamo, un enlace a su fotografía general, su fecha de entrada y observaciones.

Por otra parte, la sigla ES-07-xx fue asignada al primer material descubierto de El Soplao, unas cincuenta inclusiones procedentes de prospecciones superficiales del yacimiento. Este material fue depositado provisionalmente en el Museo Geominero del Instituto Geológico y Minero de España (IGME), en Madrid. Cada muestra con sigla ES-07-xx obtiene su sigla CES a medida que su lugar de depósito cambia. No obstante, los ejemplares descritos de rafidióptero y algunos mosquitos ceratopogónidos de las publicaciones Pérez-de la Fuente et al. (2010) y Pérez-de la Fuente et al. (2011) (anexos I.3 y I.5, respectivamente), tres de ellos holotipos, se

hallan aún en proceso de cambio de lugar de depósito y es por ello que no tienen asignada aún sigla CES (véase el final del listado proporcionado en el anexo II). La totalidad del material temporalmente depositado en el IGME será depositado definitivamente en la colección institucional de El Soplao en Cantabria.

◂ **Fig. 7.** Pieza de ámbar preparada de El Soplao con 24 sininclusiones detectadas (en su mayoría himenópteros), sigla CES 530. Escala = 5 mm. Fotografía por Rafael López del Valle.

3.3. Trabajo de gabinete: técnicas para el estudio del ámbar

Se han utilizado varias técnicas para el estudio del ámbar y sus bioinclusiones en este Proyecto de Tesis Doctoral. Éstas se exponen a continuación.

3.3.1. Microscopía de campo claro (microscopio y lupa binocular)

El uso del microscopio permite la observación de estructuras del orden de décimas de micra y una mejor definición de los detalles morfológicos, mientras que la lupa binocular, gracias a la visión estereoscópica que proporciona, resulta más útil para la toma de contacto con la inclusión y la comprensión de la disposición de sus partes anatómicas en el espacio. Por otra parte, es imprescindible contar con un buen sistema de iluminación, con luz transmitida y varios focos de luz incidente.

3.3.2. Microscopía de fluorescencia/confocal

Esta microscopía se ha utilizado para el estudio de estructuras con tamaños próximos a las decenas de micra. Se usaron para determinar la naturaleza de las estructuras que forman

parte del *trash packet* de la larva de neuróptero crisopoide, que resultaron ser tricomas de afinidad con los helechos del grupo de las gleicheniáceas (véase Pérez-de la Fuente et al., 2012e, *reenviado a la revista tras informe favorable de revisores*: anexo I.11). Además, la técnica se usó para intentar detectar señal en hebras presuntamente correspondientes a telarañas (apartado B.1.3), así como para llevar a cabo una primera evaluación de microinclusiones fúngicas (apartado 6.4.1). Estos análisis se han llevado a cabo en colaboración con la Dra. Mariela Speranza, usando un equipo Zeiss Axio Imager D1 gestionado por el Dr. Jacek Wierzchos del CCMA-CSIC (Madrid).

3.3.3. Cámara clara

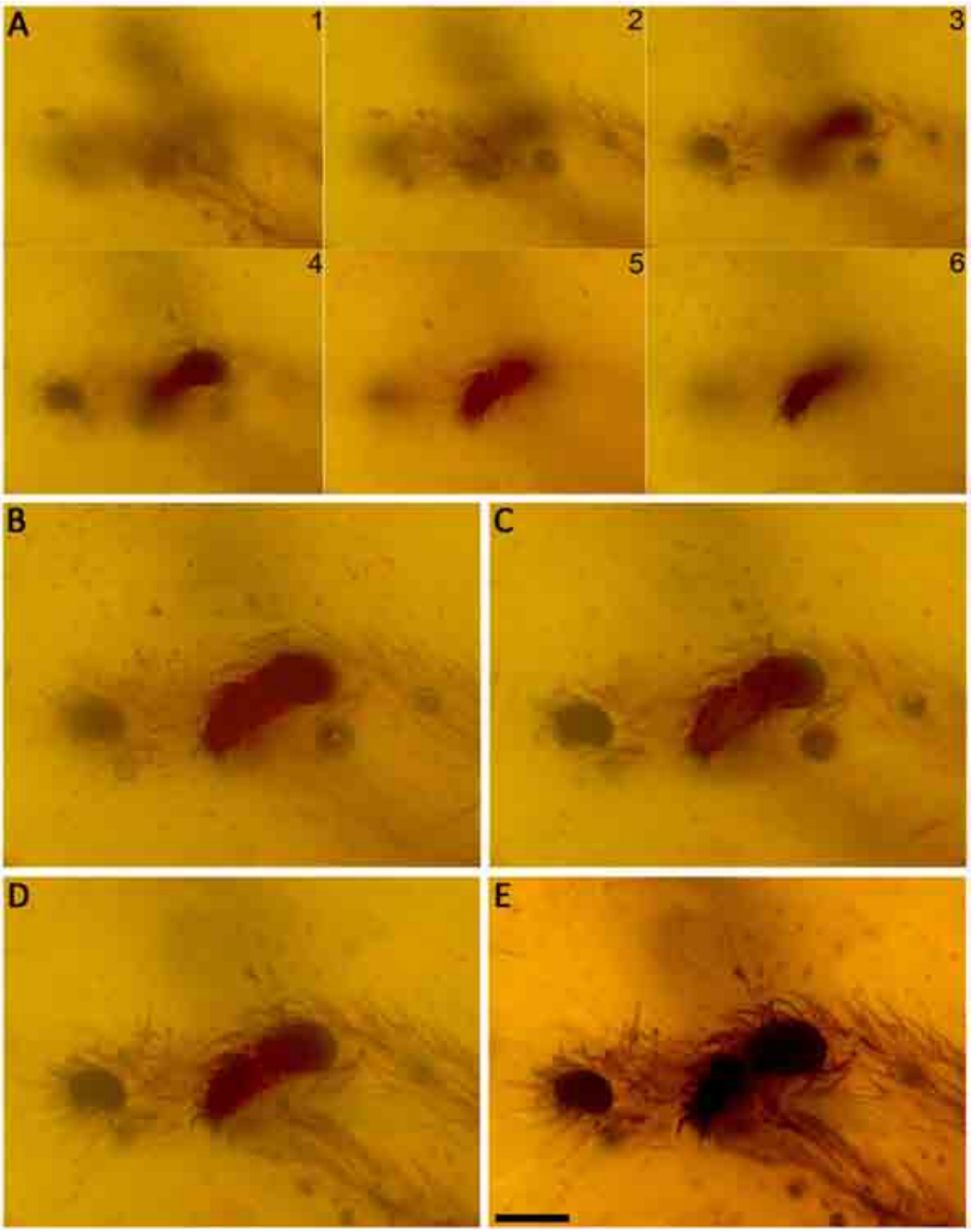
Pese a ser una técnica clásica, el dibujo científico con cámara clara sigue siendo hoy día imprescindible en Paleontología. El dispositivo superpone la imagen del ejemplar vista a través del ocular del microscopio o la lupa binocular, con la del lienzo que se capta a través de la cámara clara, permitiendo el calco de las formas que componen la imagen del ejemplar. Posteriormente, para mejorar el contraste y la limpieza de los trazos, el dibujo inicial a lápiz se redibuja a tinta sobre papel vegetal o de poliéster. El dibujo tintado finalmente se digitaliza y se ajusta al tamaño deseado para su publicación. El uso de microscopio o lupa binocular con una cámara clara viene dado por el tamaño de la inclusión a dibujar, así como por el nivel de detalle que se busca o por la dificultad para resolver ciertas estructuras, como membranas alares superpuestas o apéndices de difícil visibilidad. El uso del microscopio es muy útil pues permite discernir entre planos focales muy contiguos jugando con el enfoque micrométrico.

3.3.4. Obtención de imágenes

La obtención de fotografías se ha realizado mediante cámaras fotográficas acopladas a los instrumentos ópticos. La obtención de imágenes compuestas (o *merged images*) a partir de la combinación en una sola imagen de planos focales sucesivos es un procedimiento especialmente importante para la fotografía de estructuras en ámbar. Se han obtenido mediante retoque manual con el uso del software Helicon Focus v. 4.2.1. Consiste en la selección activa con el puntero del ratón de aquellas áreas correspondientes a estructuras del fósil que aparecen enfocadas en cada toma individual de los diferentes planos focales (Fig. 8). Pese a su laboriosidad, el resultado ha sido óptimo, sobre todo para aquellas imágenes de mayor detalle compuestas por un mayor número de planos focales en los que los procedimientos automáticos con el uso de un software son poco eficaces debido a los problemas que generan los artefactos presentes el ámbar, las preservaciones diferenciales, las alteraciones de los niveles de iluminación o la emergencia de brillos a lo largo del eje Z, entre otros.

3.3.5. Microtomografía por contraste de fase con luz sincrotrón

Esta técnica permite la obtención de modelos tridimensionales de las bioinclusiones. Sus ventajas respecto a los métodos ópticos convencionales son varias, y han significado una



▲ **Fig. 8.** Proceso de obtención de imágenes compuestas mediante uso del programa Helicon Focus v.4.2.1 a partir de imágenes tomadas en sucesivos planos focales. En el ejemplo, las imágenes compuestas son el resultado del procesado de 68 imágenes tomadas de los dos primeros pares de patas de la araña *Spinomegops arcanus* Pérez-de la Fuente, Saupe & Selden, 2012 (familia †Lagonomegopidae). Escala = 0,1 mm (mostrada en E). **A.** Seis tomas de distintos planos focales a lo largo del eje Z de la estructura de las patas, de mayor a menor profundidad focal (números de 1 a 6, respectivamente). **B.** Imagen compuesta obtenida mediante el método de *single pass based on weigthed average*. Parámetros: radio 8, suavizado 4. **C.** Imagen compuesta obtenida mediante el método de *double pass based on depth map*. Parámetros: radio 8, suavizado 4. **D.** Imagen compuesta obtenida mediante retoque manual. **E.** Imagen anterior con los niveles de brillo y contraste modificados.

revolución en Paleontología (Tafforeau et al., 2006). La técnica es especialmente adecuada para obtener imágenes de las bioinclusiones en ámbar opaco o que están rodeadas de impurezas como detritus o burbujas, ya que por medios convencionales sería imposible su observación y estudio. La técnica se ha revelado muy adecuada para el estudio del ámbar de Francia, que es opaco en más de un 80% de los casos (Perrichot, 2004). Por otra parte, el modelo tridimensional obtenido puede orientarse a voluntad, y por tanto es posible evaluar caracteres que no se pueden visualizar con el microscopio, algunos de los cuales son muy relevantes en taxonomía. Finalmente, la técnica permite llevar a cabo disecciones virtuales con las que observar caracteres internos de la inclusión como los nervios, la estructura interna del ojo compuesto, los restos momificados de la musculatura, las membranas alares bajo los élitros o las estructuras genitales internas. La disección virtual permite también retirar elementos que pueden impedir la visualización de otros, como por ejemplo patas que impiden observar estructuras torácicas.

Mediante fuentes de luz sincrotrón de tercera generación es posible obtener un haz de rayos X parcialmente coherente que, al contactar con las superficies de la muestra, crea patrones de interferencia que se propagan en el espacio. Además, aumentando la distancia entre la muestra y el detector (efecto de propagación de contraste de fase) es posible detectar un contraste mejorado de las superficies de la muestra. El procedimiento se resume a continuación. Tras detectar la posición de la bioinclusión, se realiza una tomografía (usando de 1500 a 2000 proyecciones sobre 180 grados de rotación sobre la muestra, con una resolución variable desde los 0.28 micrones), en la que la energía y la distancia muestra-detector se adaptan a las características de la muestra. Estos datos se reconstruyen posteriormente mediante algoritmos adaptados a microtomografía local. El volumen reconstruido se segmenta manualmente mediante regiones de interés con el programa VGStudioMax (Volume Graphics, Germany). Finalmente, el modelo anatómico virtual resultante, si procede, se imprime en plástico a escala mediante una impresora adaptada o se graba en cristal mediante láser a escala, lo que permite observar tanto su exterior como su interior. El protocolo establece para las descripciones taxonómicas formales a partir de segmentaciones con sincrotrón que sus modelos en plástico queden depositados en las instituciones científicas junto a sus correspondientes holotipos (Lak et al., 2008).

El tiempo a emplear en la segmentación manual de los datos y la calidad de los resultados dependen en gran medida de la conservación de la bioinclusión (es decir, de la integridad de la cutícula, que afecta a la continuidad espacial de las áreas en la tomografía y a los volúmenes posteriores en la segmentación) y de la presencia de impurezas en la matriz de ámbar, puesto que añaden ruido. La mayoría de las muestras de El Soplao que se han intentado digitalizar hasta la fecha han dado un resultado poco satisfactorio, seguramente a causa de la naturaleza de la conservación de la cutícula de las bioinclusiones. Además, un factor que disminuye la efectividad de la técnica es si el organismo incluído se rellenó de resina y por tanto existe ámbar en su interior, hecho que disminuye el contraste de las microtomografías.

Esta tarea se ha realizado gracias a siete estancias en la European Synchrotron Radiation Facility (ESRF) en Grenoble, de unos siete días de duración media (durante diciembre

de 2009, enero, febrero, abril y noviembre de 2010, julio de 2011 y julio de 2012), durante las cuales se han aprendido las técnicas a nivel usuario y se ha procedido a la digitalización del material del ámbar de España. La técnica se detalla en los artículos de Soriano et al. (2010: anexo I.4) y Saupe et al. (2012: anexo I.9). Una araña palpimanoidea ha sido también estudiada con esta técnica (véase el anexo IV).

3.3.6. Espectroscopía infrarroja transformada de Fourier (IRTF)

La espectroscopía infrarroja permite la caracterización de una sustancia orgánica a partir del grado de absorción de luz infrarroja de los elementos que forman sus compuestos químicos orgánicos y su conformación espacial, debida a la distinta naturaleza de sus enlaces. Se obtiene un espectro característico de transmitancias o absorbancias (según convenga ya que la primera es cuantitativa y la segunda cualitativa) en el que se muestran los picos de absorción para cada una de las longitudes de onda en las que la muestra absorbe el infrarrojo (Beck, 1999). Esta técnica es importante para la comparación entre ámbares de diferentes yacimientos y edades, puesto que el espectro varía en función de factores como el árbol productor de la resina y el grado de maduración del ámbar (McKellar et al., 2008). La resolución de la técnica no permite una comparación satisfactoria entre ámbares de procedencia regional y de la misma época geológica (o con historias geológicas comunes). En este sentido, la técnica se aplicó para la caracterización del ámbar de El Soplao y su contextualización con el resto de ámbares cretácicos descritos (véase Najarro et al., 2009: anexo I.1).

3.3.7. Análisis filogenético de parsimonia

Se ha llevado a cabo en el estudio mostrado en el anexo IV, utilizando una matriz de 44 caracteres para un total de 16 taxones (fósiles y actuales). Para ello, se usaron los programas PAUP* Portable version 4.0b10 para Unix y TNT (Tree analysis using New Technology), obteniéndose el mismo cladograma consenso en ambos.

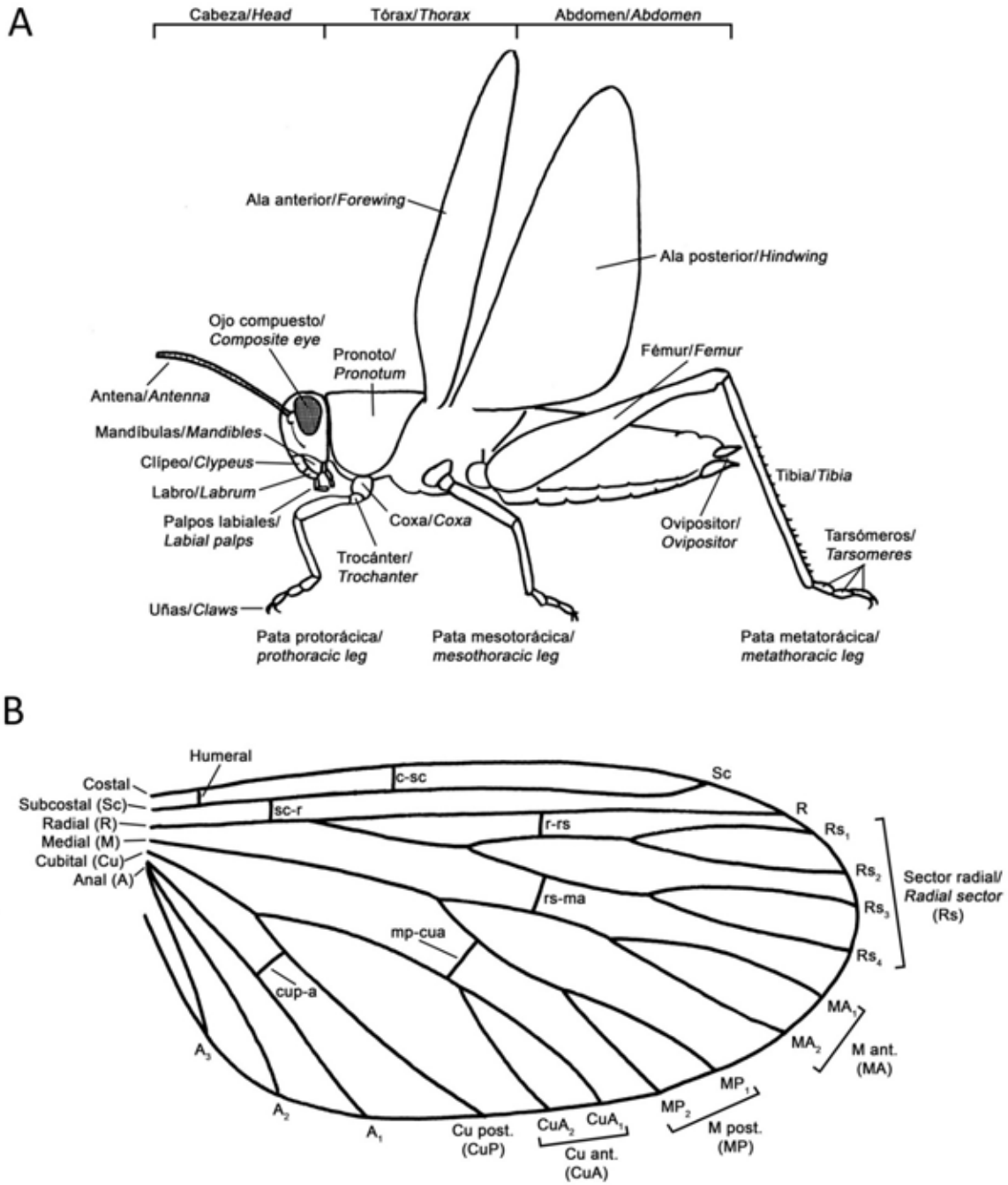
3.4. Terminología

A continuación se indica la terminología general que se usa para la descripción de los dos grandes grupos de artrópodos estudiados en los artículos que conforman este Proyecto de Tesis Doctoral: insectos y arañas. Las figuras 9 y 10 muestran esquemas idealizados de un insecto y una araña, respectivamente. Las descripciones siguen un orden anatómico anteroposterior y procuran ir de lo general a lo particular. En algunos casos, para las diagnosis, o selección de aquellos caracteres que definen un nuevo taxón y que lo distinguen de otros de su mismo rango taxonómico, se optó por una caracterización de tipo diferencial, basada en la contraposición de los caracteres del taxón descrito con aquellos caracteres de los taxones más afines de los cuales se quiere diferenciar. En otros casos, se optó por establecer diagnosis de tipo descriptivo, menos restrictivas por utilizarse un mayor número de caracteres.

3.4.1. Caracteres con importancia taxonómica de los grupos de artrópodos estudiados

Insectos (Clase Insecta) (Fig. 9). Obedeciendo a la gran disparidad morfológica de los diferentes órdenes de insectos, existen caracteres concretos con importancia taxonómica para cada uno de ellos. Ello se especifica entre corchetes usando las siguientes abreviaciones: Raphidioptera = R; Neuroptera = N, Diptera (Ceratopogonidae) = C; Hymenoptera (Megalyridae, Evaniidae) = M.

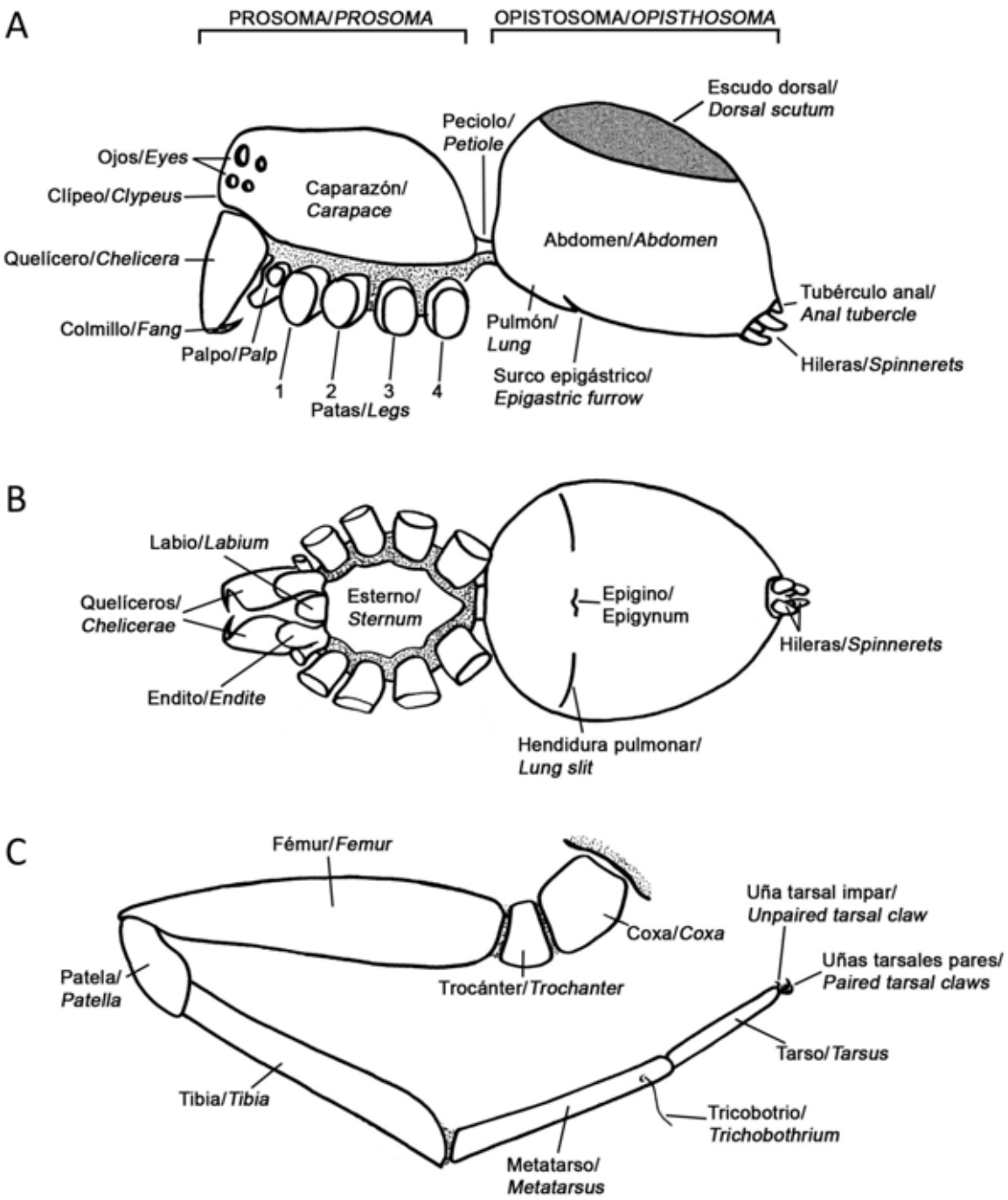
- *Cabeza:* morfología general [R, N].
- *Antenas:* número de antenómeros; morfología del escapo, pedicelo y antenómeros; presencia de elementos sensitivos (sensilias).
- *Ojos compuestos:* tamaño en relación a la cabeza [R], unión/separación de los ojos dorsomedialmente [C].
- *Ocelos:* ausencia/presencia y disposición relativa de los tres ocelos formando un triángulo [R].
- *Piezas bucales:* número y morfología de los palpómeros [C], desarrollo de las piezas bucales y dentición/serrulación asociada [C], número de dientes mandibulares y su simetría respecto a ambas mandíbulas [M].
- *Thorax/Mesosoma (en Hymenoptera):* morfología y presencia de ornamentación o surcos en los distintos escleritos del mesosoma [M], presencia de tubérculos setados en adultos [N].
- *Ala:* presencia de setas (macrotricos) en la membrana alar [C]; posición, distribución y tipo según grado de desarrollo (espectral tubular, etc.) de las venas alares; morfología de las celdillas que conforman las venas alares; número y posición de venas transversas (Fig. 9B).
- *Patas:* tamaño relativo de los podómeros; presencia, localización y abundancia de estructuras cuticulares como espinas o espolones; pigmentación [R],
- *Uñas:* presencia y morfología de estructuras accesorias como dentículos basales [C].
- *Estructuras genitales:* morfología y disposición relativa de cada uno de los escleritos genitales (muy específico para cada grupo).



▲ **Fig. 9.** Morfología general de un insecto con indicación de la nomenclatura usada para las diferentes estructuras en castellano e inglés. **A.** Morfología corporal, tomando como modelo un ortóptero caelífero en vista lateral. **B.** Diagrama de un ala de insecto idealizada, con la nomenclatura de la venación más comúnmente utilizada (resultado de variaciones del modelo clásico de Comstock-Needham, 1898). Entre paréntesis, las abreviaciones de las principales venas. Las venas transversas se simbolizan con el nombre de las venas principales que unen, en minúsculas y separadas por un guión. ant. = anterior, post. = posterior.

Arañas (Clase Arachnida, Orden Araneae) (Fig. 10)

- *Caparazón:* elevación; morfología de contorno (piriforme, ovoide, etc.); presencia y morfología de la fóvea (alargada, una o dos depresiones).
- *Ojos:* número (seis u ocho); conformación; tamaño relativo.
- *Clípeo:* altura; proyección (hacia delante o recto).
- *Quelíceros:* tamaño; proyección (hacia delante, atrás, o recto); presencia y forma de *peg teeth* (= setas engrosadas en el margen interno de los quelíceros), posición de los *peg teeth* (opuestos a la punta del colmillo o también presentes en el paturón, es decir, la región proximal del quelícero); presencia de órganos estridulatorios.
- *Piezas bucales (labio y enditos):* morfología; orientación; presencia de muescas en la base del labio, presencia de serrula (una o varias hileras de dentículos) en el margen distal externo de los enditos.
- *Esterno:* forma (alargada, en forma de escudo, etc.); morfología del margen (indentado, sinuoso, liso); presencia de ornamentación (rugosidad).
- *Opistosoma:* morfología (globulosa, alargada); presencia y localización de áreas esclerotizadas.
- *Hileras:* número (dos, cuatro o seis); disposición; tamaño relativo.
- *Patas:* tamaño relativo de los podómeros; *leg formula* (= número de 4 dígitos formado por cifras del 1 al 4 correspondiente a la ordenación de las patas por su longitud total, de mayor a menor. En el ejemplo "1243", la pata 1 es la de mayor longitud y la pata 3 la de menor); presencia, localización y abundancia de estructuras cuticulares como espinas o setas espatuladas.
- *Uñas:* presencia de uña impar, número de filas de uñas pares.
- *Tricobotriotaxia:* número, posición, y longitud de tricobotrios (= mecanorreceptores filiformes) en patas y palpos.
- *Palpos masculinos (órgano copulador):* tipo de palpo (haplogino - simple vs. entelegino - complejo), morfología del cimbio (= tarso palpal modificado); morfología del bulbo (= reservorio de esperma que emerge del cimbio, pudiendo ser expansible); presencia y morfología de apófisis (émbolo, conductores, etc.); presencia de estructuras cuticulares (con función estridulante o no).



▲ **Fig. 10.** Morfología general de una araña con indicación de la nomenclatura usada para las diferentes estructuras en castellano e inglés. **A.** Vista lateral. **B.** Vista ventral. **C.** Esquema de una pata. Nótese como las patas y palpos se muestran cortados en las subfiguras A y B, y la setación ha sido omitida en todas las subfiguras (redibujado y modificado de Foelix, 2011).

4.2. Nomenclatura abierta

En Taxonomía, y más comúnmente en Taxonomía Paleontológica, es común el uso de nomenclatura abierta, mediante la cual se indica el grado de certidumbre respecto a la determinación taxonómica propuesta (Bengtson, 1988).

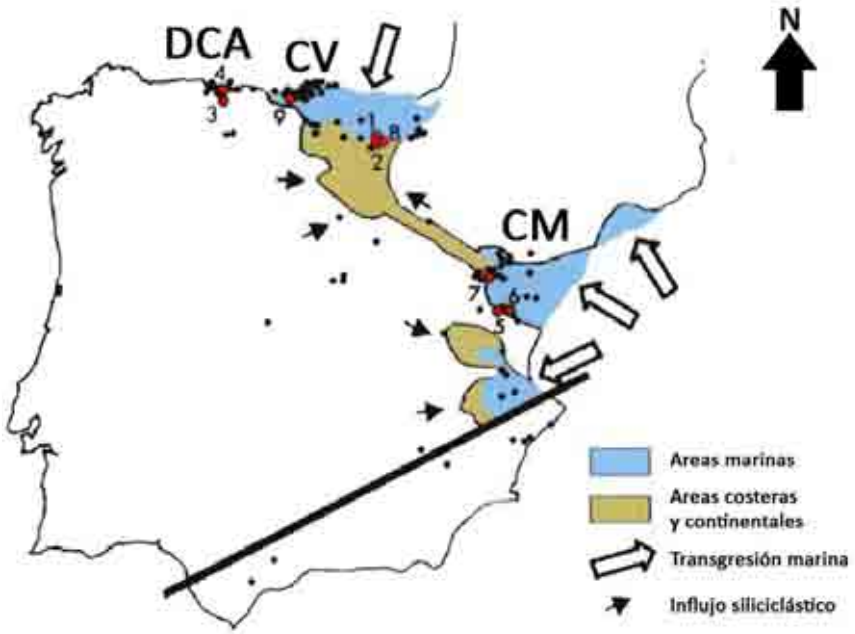
Cuando no es posible o no se quiere alcanzar el rango de especie en una determinación taxonómica, se usa "sp." tras el epíteto genérico. Ejemplo: *Austroconops* sp. (véase Pérez-de la Fuente et al., 2011: anexo I.5).

Cuando la asignación taxonómica es incierta y por lo tanto tiene carácter provisional, debido principalmente a restricciones en cuanto a la conservación del fósil o bien a su estatus taxonómico problemático (normalmente a nivel génerico), se usa un signo de interrogación ("?"). Ejemplos: *Styporaphidia*? *hispanica* (véase Pérez-de la Fuente et al., 2012a: anexo I.6); *Lagonomegops*? *cor* (véase Pérez-de la Fuente et al., 2012d, *en prensa*: anexo I.10).

4. MARCO GEOLÓGICO

4.1. Contexto geológico y paleobiogeográfico

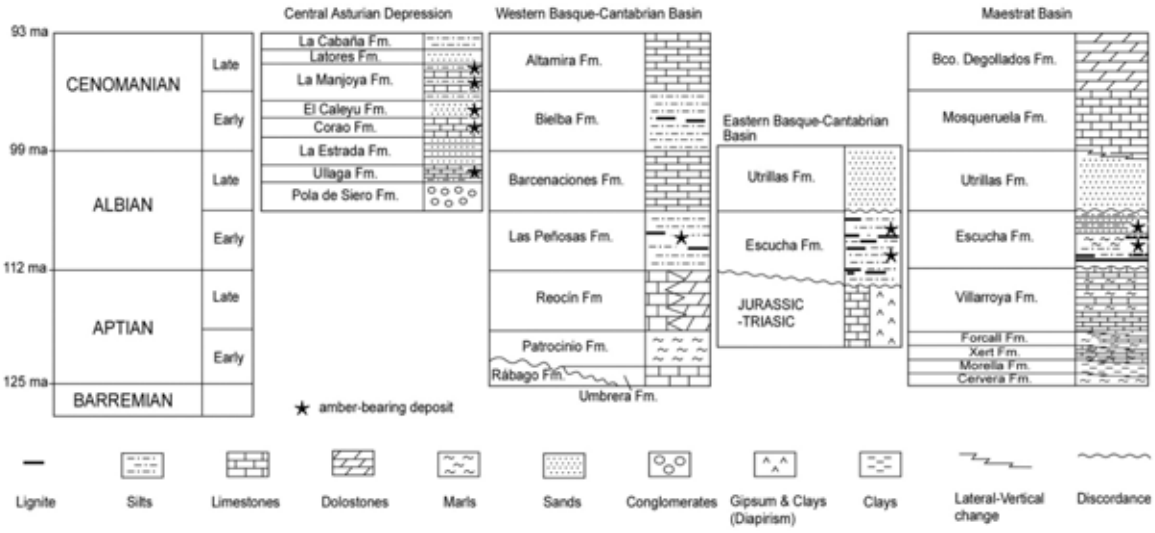
Desde el Jurásico Inferior, y durante unos 100 millones de años, la Placa Ibérica presentó un aislamiento geográfico insular, en un emplazamiento latitudinal más meridional que en la actualidad (véase Blakey, 2011). Durante el intervalo Oxfordiense (Jurásico Superior) - Albiense (Cretácico Inferior), tuvo lugar un proceso de *rifting* entre la Placa Ibérica y la Placa Europea asociado a la apertura del Atlántico norte (Martín-Chivelet et al., 2002). La Placa Ibérica se localizaba entonces en la frontera climática entre un clima con estaciones marcadas, presentando un periodo estacional seco y otro húmedo, y un clima paratropical (Fig. 1; Scotese, 2000).



▲ **Fig. 11.** Yacimientos de ámbar cretácico en España situados sobre un mapa paleogeográfico de la Península Ibérica correspondiente al Aptiense Superior-Albiense Inferior. Se marcan con puntos negros unas cien localidades cretácicas que han brindado ámbar. Los nueve yacimientos que a día de hoy han proporcionado macrobioinclusiones se han marcado en rojo, y son, en orden cronológico de descubrimiento: (1) Peñacerrada I (Moraza, Burgos), (2) Peñacerrada II (Peñacerrada-Montoria, Álava), (3) El Caleyu (El Caleyu, Asturias), (4) Pola de Siero (Pola de Siero, Asturias) , (5) Arroyo de la Pascueta (Rubielos de Mora, Teruel), (6) La Hoya (Cortes de Arenoso, Castellón), (7) San Just (Utrillas, Teruel), (8) Salinillas de Buradón (Salinillas de Buradón, Álava) y (9) El Soplao (Rábago, Cantabria). DCA: Depresión Central Asturiana; CV: Cuenca Vasco-Cantábrica; CM: Cuenca del Maestrazgo. Figura modificada de Peñalver & Delclòs (2010), a su vez basada en Mas et al. (2004).

En España, la mayoría de los yacimientos cretácicos de ámbar se hallan localizados en una línea de paleocosta que cruza el cuadrante noreste de la Península Ibérica. Se sitúan, básicamente, en la Cuenca del Maestrazgo (o Maestrat), con salida al mar de Tethys, y la Depresión Central Asturiana y la Cuenca Vasco-Cantábrica, con salida al proto-Atlántico (Fig. 11). Los yacimientos de ámbar suelen estar asociados a carbón depositado en ambientes de

llanura deltaica, como los pantanos y ambientes fluviales (con influencia marina esporádica) de la Cuenca del Maestrazgo, o como los depósitos de clara influencia marina de la Depresión Central Asturiana y la Cuenca Vasco-Cantábrica (Peñalver & Delclòs, 2010). Todos los ámbares que a día de hoy han proporcionado macrobioinclusiones tienen una edad Albiense (la mayoría de ellos con un edad circunscrita a 110-105 millones de años (Fig. 12). Las dataciones del ámbar y su contenido paleobiológico se han basado en el contenido polínico, teniendo en cuenta que no se han observado evidencias de procesos de reelaboración en los depósitos sedimentarios que lo contiene (ibid.).



▲ **Fig. 12.** Secciones cronoestratigráficas de las unidades litológicas del Cretácico Inferior-Cretácico Superior de la Península Ibérica en donde se ha encontrado ámbar. Tan sólo se han hallado macrobioinclusiones en los ámbares del Albiense. Extraído de Peñalver & Delclòs, 2010.

La Cuenca del Maestrazgo está limitada por fallas lístricas que se formaron durante el proceso de *rifting* (Oxfordiense-Albiense) entre la Placa Ibérica y la Placa Europea. Durante el Cretácico Inferior tiene lugar una sedimentación dominada por arenas, limos y arcillas, depositados en ambientes deltaicos y de pantanal (Querol & Salas, 1988; Querol et al., 1992; Delclòs et al., 2007). Los yacimientos de ámbar con bioinclusiones de La Hoya, Arroyo de la Pascueta y San Just (Fig. 13) se incluyen en la Fm. Escucha, correspondiente al final de la etapa de *rifting*, durante el Albiense. La Fm. Escucha se ha subdividido tradicionalmente en tres miembros que aparecen en continuidad sedimentológica: de base a techo, el Miembro Barriada, el Miembro Regachuelo y el Miembro La Orden. Los depósitos de ámbar han sido hallados principalmente a techo del Miembro Regachuelo, por encima de los niveles de explotación de carbones y, ocasionalmente, en la base del Miembro La Orden (Alcalá et al., 2009). El yacimiento de San Just se sitúa aparentemente en la transición entre el Miembro Regachuelo y el Miembro La Orden (Peñalver et al., 2007; Alcalá et al., 2009; Villanueva-Amadoz et al., 2010). Otros autores (Rodríguez-López et al., 2012) han propuesto que se desarrolló un sistema desértico arenoso (Erg) durante el Cretácico en esta zona, interpretado a partir de estudios estratigráficos, sedimentológicos, paleoclimáticos, paleogeográficos y de relación tectónica-sedimentación de las formaciones Escucha y Utrillas. Estos estudios indican

que los potentes tramos arenosos, con tramos arcillosos y limosos del Miembro La Orden, y la totalidad de la Fm. Utrillas, en su área tipo y sectores adyacentes, constituyen el registro sedimentario del primer Erg del Cretácico de Europa. El Erg se desarrollaría por encima de la Superficie de Discontinuidad Regional (SDR) que se encuentra estratigráficamente dentro del registro de la Fm. Escucha y marca la desaparición regional de los tramos de carbón que se explotan en la Comarca de la Cuencas Mineras de Teruel (Fig. 13A). Esta superficie está asociada a procesos de exposición subaérea, erosión y tectónica sinsedimentaria. La SDR se encontraría en el yacimiento de San Just por encima de los niveles con ámbar, dentro de lo que los autores consideran como Sucesión Sedimentaria Inferior (SSI) formada principalmente por arcillas y limos (Fig. 13A).

▲ **Fig. 13.** Yacimientos de ámbar de la Cuenca del Maestrazgo. **A**. Yacimiento de San Just, en Utrillas (Teruel). **B**. Yacimiento de La Hoya, en Cortes de Arenoso (Castellón). SDR: Superficie de Discontinuidad Regional. SSI: Sucesión Sedimentaria Inferior. Fotografías por Xavier Delclòs.

La edad de los yacimientos de La Hoya, Arroyo de la Pascueta y San Just, basada en estudios palinológicos (Solé de Porta et al., 1994) y amonites (Martínez et al., 1993; Moreno-Bedmar et al., 2008), es Albiense Inferior-Medio. Otros datos basados en la palinología indican edades algo más modernas (Albiense Medio-Inferior) para el yacimiento de San Just (Villanueva-Amadoz et al., 2010).

En la Depresión Central Asturiana, los yacimientos de ámbar con macrobioinclusiones de El Caleyu y Pola de Siero (Fig. 14) se hallan incluidos en la Fm. Ullaga (Albiense Superior), que consiste básicamente en calizas, limolitas grises y margas limosas depositadas en ambientes de llanura intermareal, acompañadas de abundantes ostréidos, ostrácodos, foraminíferos, seláceos y hojas de plantas (Arbizu et al., 1999; Bernárdez, 2002; González-Fernández et al., 2004; Bernárdez et al., 2005). La edad de El Caleyu y Pola de Siero según los datos aportados por las asociaciones de foraminíferos y algas es Albiense Superior (González-Fernández et al., 2004).

▲ **Fig. 14.** Cantera de Pola de Siero (Asturias). Contacto entre las Formaciones Ullaga (base) y La Estrada (techo). Fotografía por Xavier Delclòs.

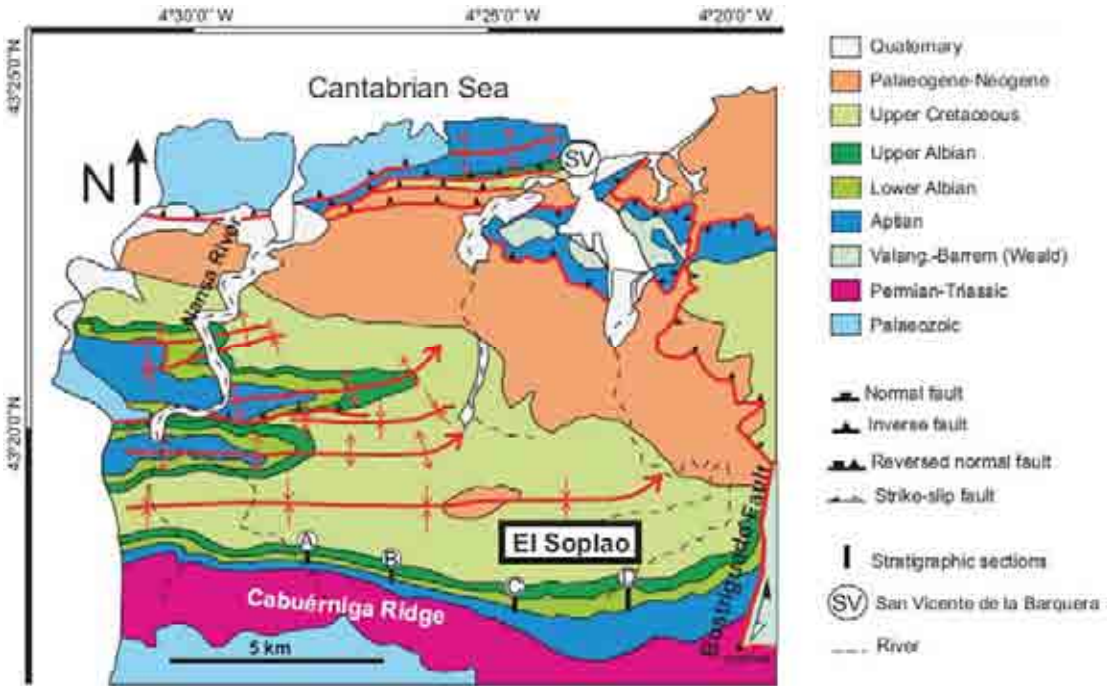
La formación de la Cuenca Vasco-Cantábrica también se asocia al proceso de *rifting* y la apertura del Atlántico norte. Los yacimientos de ámbar con macrobioinclusiones se hallan en los márgenes oriental y occidental de la cuenca. En general, los yacimientos de ámbar se relacionan con ambientes parálicos en el sector oriental de la cuenca y parálicos-marinos en su sector occidental (Peñalver & Delclòs, 2010). Los tres yacimientos del margen oriental de la Cuenca Vasco-Cantábrica que han brindado ámbar con contenido en macrobioinclusiones son Peñacerrada I, Peñacerrada II y Salinillas de Buradón (Fig. 15). Estos yacimientos se incluyen en la Fm. Escucha, que se subdivide aquí en tres subunidades que no se pueden correlacionar directamente con los tres miembros reconocidos en la Cuenca del Maestrazgo. La Fm. Escucha se halla representada en el área de Peñacerrada por una sucesión deltaica en las subunidades inferior y media, y una trasgresión vertical en la subunidad superior (Martínez-Torres et al., 2003). Los yacimientos de Peñacerrada I y Peñacerrada II se sitúan en la subunidad media de la Fm. Escucha, que contiene abundantes niveles lutíticos y arcillosos grises ricos en carbón a techo de las secuencias de relleno de bahías interdistributarias. Dicha subunidad se caracteriza por arcosas y microconglomerados silícicos de relleno de canal, y abundantes niveles de carbón, originados durante el periodo de transición entre la máxima transgresión marina y el inicio de la regresión y la correspondiente progradación deltaica (ibid.). Para los yacimientos

de Peñacerrada I y Peñacerrada II, los datos palinológicos indican una edad de Albiense Inferior (Barrón et al., 2009).

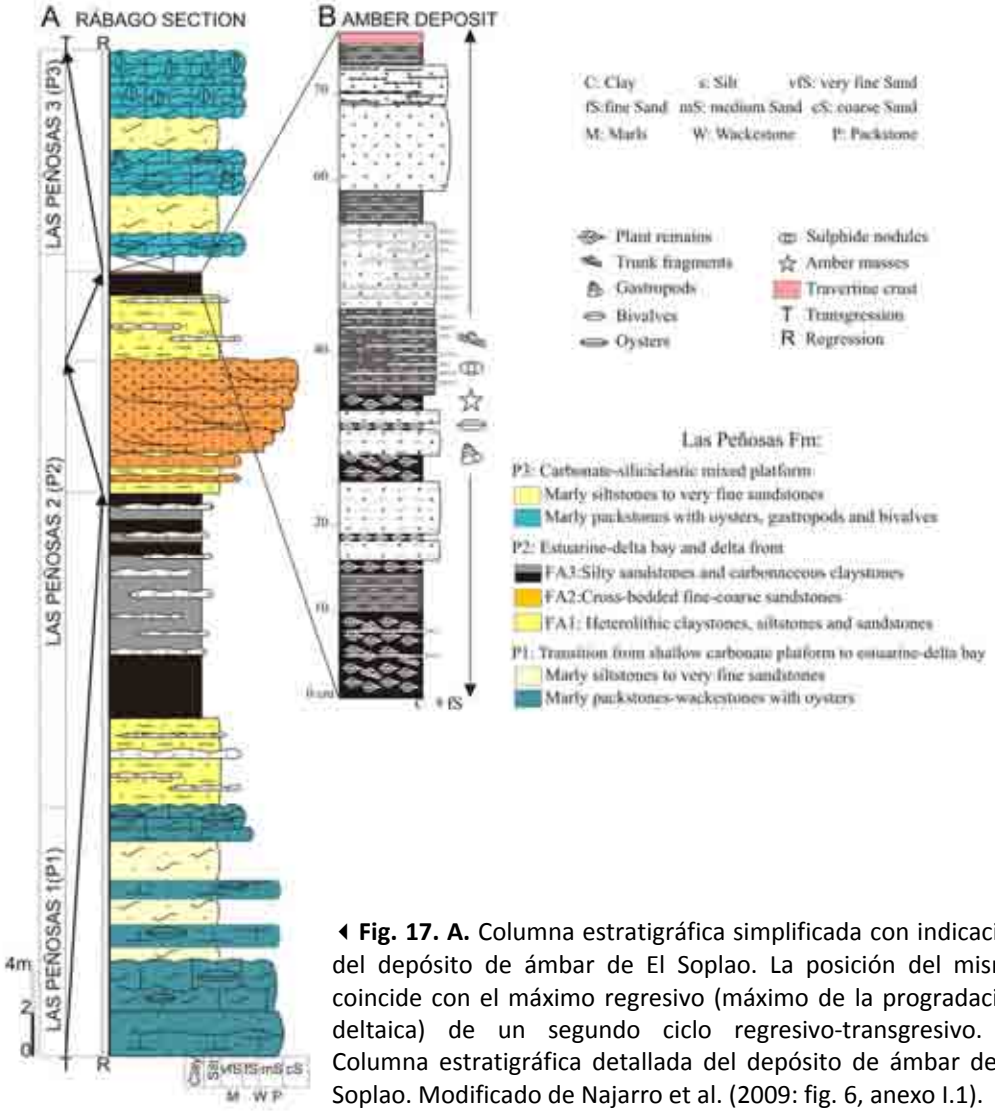
▲ **Fig. 15.** Yacimientos de ámbar del margen oriental de la Cuenca Vasco-Cantábrica. **A**. Yacimiento de Peñacerrada I (Moraza, Burgos). **B**. Yacimiento de Peñacerrada II (Peñacerrada-Montoria, Álava). **C**. Yacimiento de Salinillas de Buradón (Álava) (flecha), visto desde San Felices (La Rioja). Fotografías por Xavier Delclòs.

El yacimiento de El Soplao se ubica en el margen occidental de la Cuenca Vasco-Cantábrica, en la denominada cuenca Norcantábrica (Fig. 16), cerca del municipio de Rábago, en Cantabria. Estratigráficamente, el yacimiento se incluye en la Fm. Las Peñosas, una unidad siliciclástica continental a transicional marina intercalada dentro de una secuencia marina regresiva-transgresiva, predominantemente carbonatada, de edad Aptiense Inferior - Albiense Inferior (Fig. 17; Najarro et al., 2009: anexo I.1). La Fm. Las Peñosas corresponde a un estadio regresivo máximo de esta secuencia, y tiene una edad de Albiense Inferior.

El yacimiento de El Soplao se halla localizado estratigráficamente en una unidad de areniscas y limolitas heterolíticas y lutitas carbonosas depositadas en ambientes estuarinos y deltaicos con clara influencia marina (Najarro et al., 2009: anexo I.1). Las piezas de ámbar aparecen acumuladas en un nivel de 0,7 a 2,5 m de espesor, mayoritariamente de arcillas ricas en materia orgánica y niveles más carbonatados.



▲ **Fig. 16.** Mapa geológico detallado de la subcuenca Norcantábrica en el área del yacimiento de El Soplao. Modificado de Najarro et al. (2009: fig. 3C, anexo I.1).



◀ **Fig. 17. A.** Columna estratigráfica simplificada con indicación del depósito de ámbar de El Soplao. La posición del mismo coincide con el máximo regresivo (máximo de la progradación deltaica) de un segundo ciclo regresivo-transgresivo. **B.** Columna estratigráfica detallada del depósito de ámbar de El Soplao. Modificado de Najarro et al. (2009: fig. 6, anexo I.1).

En asociación con el ámbar se encuentran variados restos paleontológicos que se describen en el apartado 4.2. Una exposición detallada de la estratigrafía y sedimentología del yacimiento puede consultarse en Najarro et al. (2009, 2010: anexos I.1 y I.2).

▲ **Fig. 18.** Aspecto de los niveles con contenido en ámbar en el yacimiento de El Soplao y ámbar *in situ.* **A.** Aspecto general de la calicata principal en donde se llevó a cabo una extracción manual de piezas de ámbar y luego un lavado directo con agua a presión (marzo de 2009). **B.** Aspecto de los niveles arcillosos y carbonatados de concentración de ámbar, y un nivel arenoso subyacente. **C.** Lignito (azabache) asociado al ámbar. **D.** Nivel laminado de concentración de cutículas de plantas, sobre todo de *†Frenelopsis* sp. y ginkgoales. **E-F.** Piezas de ámbar *in situ* en los niveles más arcillosos. Nótese la corteza opaca, color marrón, en F. **G.** Pieza de ámbar entre dos niveles arenosos. Se amplía en la subfigura **H** (nótese su intensa fluorescencia azulada). Fotografías: A, B, C, D y E por Rafael Lozano; F, G y H por Rafael López del Valle.

4.2. Material paleontológico asociado al ámbar de El Soplao

4.2.1. Palinología

El estudio palinológico preliminar del yacimiento de El Soplao indica la existencia de bosques de coníferas adaptados una estación seca bajo un clima subtropical (Najarro et al., 2010: anexo I.2). Este estudio proporcionó 20 morfotipos de esporas de criptógamas, 18 de granos de polen de gimnospermas y seis de granos de polen de angiospermas, mostrando una diversidad regional taxonómica elevada (Najarro et al., 2010: tabla 1, anexo I.2). Los granos de polen de gimnospermas son los más abundantes, con un claro predominio de *Inaperturopollenites dubius* (Potonié & Venitz, 1932) Thompson & Pflug, 1953, afín a las familias de coníferas Cupressaceae y Taxodiaceae, y †*Classopollis* spp, de afinidad a †Cheirolepidiaceae (véase Peyrot et al., 2008). Las esporas de criptógama, mucho menos abundantes que los granos de polen de gimnosperma, presentan una diversidad dominada por *Deltoidospora* spp., afines a los helechos de las familias Cyatheaceae y Dicksoniaceae (ibid.). Asimismo, destacar la presencia de *Gleicheniidites senonicus* Ross, 1949 y *Ornamentifera peregrina* (Bolchovitina, 1953) Bolchovitina, 1968, que manifiesta la presencia de la familia de helechos Gleicheniaceae (Pérez-de la Fuente et al., 2012e, *reenviado a la revista tras informe favorable de revisores*: fig. S4, anexo I.11). Actualmente, el Dr. Eduardo Barrón, miembro del equipo de investigación AMBARES, lleva a cabo un estudio palinológico exhaustivo del yacimiento de El Soplao.

4.2.2. Meso- y macrorrestos de plantas

Los restos de compresiones cuticulares son muy abundantes en El Soplao, a menudo formando niveles de acumulación que pueden alcanzar los 10 cm de grosor (Fig. 18D; Najarro at el., 2010: fig. 7D, anexo I.2). Las cutículas más abundantes son las pertenecientes a los tallos vegetativos del género †*Frenelopsis*, de la familia †Cheirolepidiaceae. Asimismo, también se encuentran conos femeninos del género †*Alvinia,* afines al género †*Frenelopsis.* (Najarro et al., 2009: fig. 11C, E-F, P, anexo I.1). Algunos tallos vegetativos de †*Frenelopsis* se han hallado en conexión anatómica, en ramificaciones dicotómicas de hasta cuatro niveles (Fig. 19A; Najarro et al., 2010: fig. 3.5-3.6, anexo I.2). Otras cutículas de coníferas halladas son las pertenecientes al género †*Arctopitys* (antes †*Mirovia*), de la familia de coníferas †Miroviaceae, así como tallos foliados de tipo *Brachyphyllum* (Najarro et al., 2009: fig. 11D, G-H, L-M, anexo I.1). Finalmente, se encuentran también cutículas de hojas de ginkgoales asignadas a los géneros †*Nehvizdya* sp. (†*Eretmophyllum* sp. para otros autores) y †*Pseudotorellia* sp., además de óvulos asignados tentativamente al género †*Nehvizdyella* (Najarro et al., 2009: fig. 11I-K, N-O, anexo I.1).

Asimismo, se hallan abundantes restos de material lignificado en forma de fusinita con origen en incendios forestales (carbón producto de una combustión rápida) (Najarro et al., 2010: fig. 7.2, anexo I.2). La funisita, de aspecto brillante y consistencia friable, es el resultado de la pirolisis de material vegetal debido a incendios o actividad volcánica, presentando una microestructura en la que las paredes celulares han sido vitrificadas y fusionadas entre sí por efecto de las altas temperaturas (Najarro et al., 2010: fig. 7.3-7.6, anexo I.2; Scott, 2010).

Por último, destacar la presencia de raíces *in situ*, dispuestas en un patrón de disposición radial (Fig. 19B), así como rizocreciones piritizadas (Fig. 19C).

4.2.3. Invertebrados

Se han encontrado, asociados al ámbar, casts en marcasita de moluscos marinos o de agua salobre, gasterópodos y bivalvos (Fig. 19D), así como conchas de ostréidos, que conservan su biomineralización original. Por otra parte, se han hallado briozoos y tubos de serpúlido fijados a la superficie de algunas piezas de ámbar, las cuales no muestran signos de reelaboración ni retrabajamiento. Ambos tipos de restos de invertebrados se encuentran con su composición original de carbonato, mientras que algunos tubos de serpúlidos se han conservado como impresiones limoníticas, como moldes internos de marcasita y como marcas alargadas en la superficie del ámbar, según los casos (Najarro et al., 2010: fig. 8.1-8.3, anexo I.2). Las marcas alargadas se originaron al principio de la fosildiagénesis al penetrar la resina en semitubos abiertos por el lado de contacto con la masa de resina, seguramente por la acción de la presión litostática, y perderse posteriormente dichos semitubos.

▲ **Fig. 19.** Material paleontológico asociado al ámbar de El Soplao. **A**. Tallos vegetativos de †*Frenelopsis* sp. en conexión anatómica. Escala = 1 cm. **B**. Raíces *in situ* en disposición de roseta. **C.** Rizocreción piritizada. **D**. Restos de bivalvos en marcasita. Fotografías: A, B y D por Xavier Delclòs; C por Rafael Lozano.

5. ASPECTOS TAFONÓMICOS

5.1. Necrobiosis

5.1.1. Sesgos necrobióticos

El registro de ámbar se halla sesgado respecto a ciertos grupos de organismos. Una serie de factores bióticos y abióticos condicionan la probabilidad con la que los organismos se exponen a la resina, entran en contacto con ella y acaban atrapados en la misma (véase Rasnitsyn & Quicke, 2002; Martínez-Delclòs et al., 2004).

Los factores bióticos dependen de la propia resina o de los organismos que pueden quedar atrapados en la misma. Las características fisicoquímicas de la resina determinan su viscosidad/fluidez y su contenido en sustancias repelentes, frente a posibles herbívoros o patógenos, o atractivas de ciertos grupos de insectos como por ejemplo los polinizadores (Langenheim, 2003). Dichas características varían en función del lugar donde la resina se secreta (véase el apartado 5.1.2).

Los factores relacionados con los organismos son morfológicos, etológicos y autoecológicos. Respecto a la morfología, el factor más determinante es el tamaño del organismo. En el ámbar suele haber un predominio de las inclusiones de organismos de pequeño tamaño (< 5mm). Cuanto más pequeño es un organismo, menor es su capacidad para vencer la adherencia a la resina y por tanto su probabilidad de acabar atrapado en la misma es mayor. De igual modo, los organismos pequeños, especialmente los insectos alados con poca capacidad de vuelo, son fácilmente arrastrados por las corrientes de aire y por tanto su probabilidad de entrar en contacto accidental con la resina es mayor. Los ámbares generados a partir de resinas producidas por angiospermas en el Cenozoico parecen mostrar una paleobiota asociada de mayor tamaño que los ámbares generados a partir de resinas en el Mesozoico, producidas principalmente por gimnospermas.

La formación de enjambres nupciales y otros comportamientos gregarios, o la propia actividad de los organismos, son características etológicas que sesgan el registro de los organismos en el ámbar. Por ejemplo, para las arañas cabe esperar un sesgo hacia aquellas formas merodeadoras, las cuales se desplazan activamente en busca de sus presas, en lugar de aquellas formas que cazan usando una telaraña y que por tanto esperan inmóviles a sus presas (Penney & Selden, 2011). Finalmente, la cercanía ecológica de los organismos a las fuentes de emisión de la resina condiciona su abundancia en el ámbar; por ello, a modo de ejemplo, los insectos xilófagos o xilófilos son relativamente abundantes en los ámbares (Martínez-Delclòs et al., 2004).

Los factores bióticos anteriores, como es de esperar, se hallan condicionados por factores abióticos (ambientales) (Langenheim, 2003). Éstos son principalmente la temperatura, la humedad, la disponibilidad hídrica y de nutrientes, y la insolación. Por ejemplo, las elevadas temperaturas y una elevada disponibilidad hídrica o de nutrientes son factores que pueden promover la secreción de resina, de ahí que ésta pueda llegar a mostrar ciclos estacionales cuando se da en climas con una estacionalidad marcada (Martínez-Delclòs et al., 2004). Otro

ejemplo es que la radiación ultravioleta promueve la polimerización de la resina y por tanto condiciona su grado de fluidez. Parte de estos factores ambientales, junto a muchos otros, a mayor escala, controla fenómenos como las tormentas o los incendios, los cuales a su vez promueven la secreción de resina al causar un daño traumático sobre las poblaciones de plantas resiníferas.

El proceso de captura efectiva por la resina puede durar desde pocos segundos a varios días, dependiendo si los organismos mueren por asfixia o por fatiga, algo que depende principalmente del tamaño del organismo y de la fluidez de la resina (Martínez-Delclòs et al., 2004).

5.1.2. Producción de resina

5.1.2.1. Plantas productoras de resina

Hoy en día, varias familias de gimnospermas y de angiospermas producen resina (Langenheim, 2003). No obstante, se sabe que los principales ámbares del Cretácico, cuando las angiospermas se hallaban en proceso de diversificación (Friis et al., 2011), fueron originados por coníferas de la familias Araucariaceae, †Cheirolepidiaceae y Cupressaceae *sensu lato* (incluyendo Taxodiaceae) (véase la Tabla 2).

Ámbar	Conífera(s) productora(as) de resina	Fuente
Líbano	Araucariaceae, Cheirolepidiaceae	Azar et al., 2010a
España (Peñacerrada I, El Soplao)	Araucariaceae?, Cheirolepidiaceae, otras	Menor-Salván et al., 2010; Peñalver & Delclòs, 2010
Myanmar	Araucariaceae	Ross et al., 2010
Francia (Archingeay-Les Nouillers)	Araucariaceae, Cheirolepidiaceae	Perrichot et al., 2010
EUA (Nueva Jersey)	Cupressaceae	Grimaldi & Nascimbene, 2010
Canadá	Cupressaceae	McKellar & Wolfe, 2010

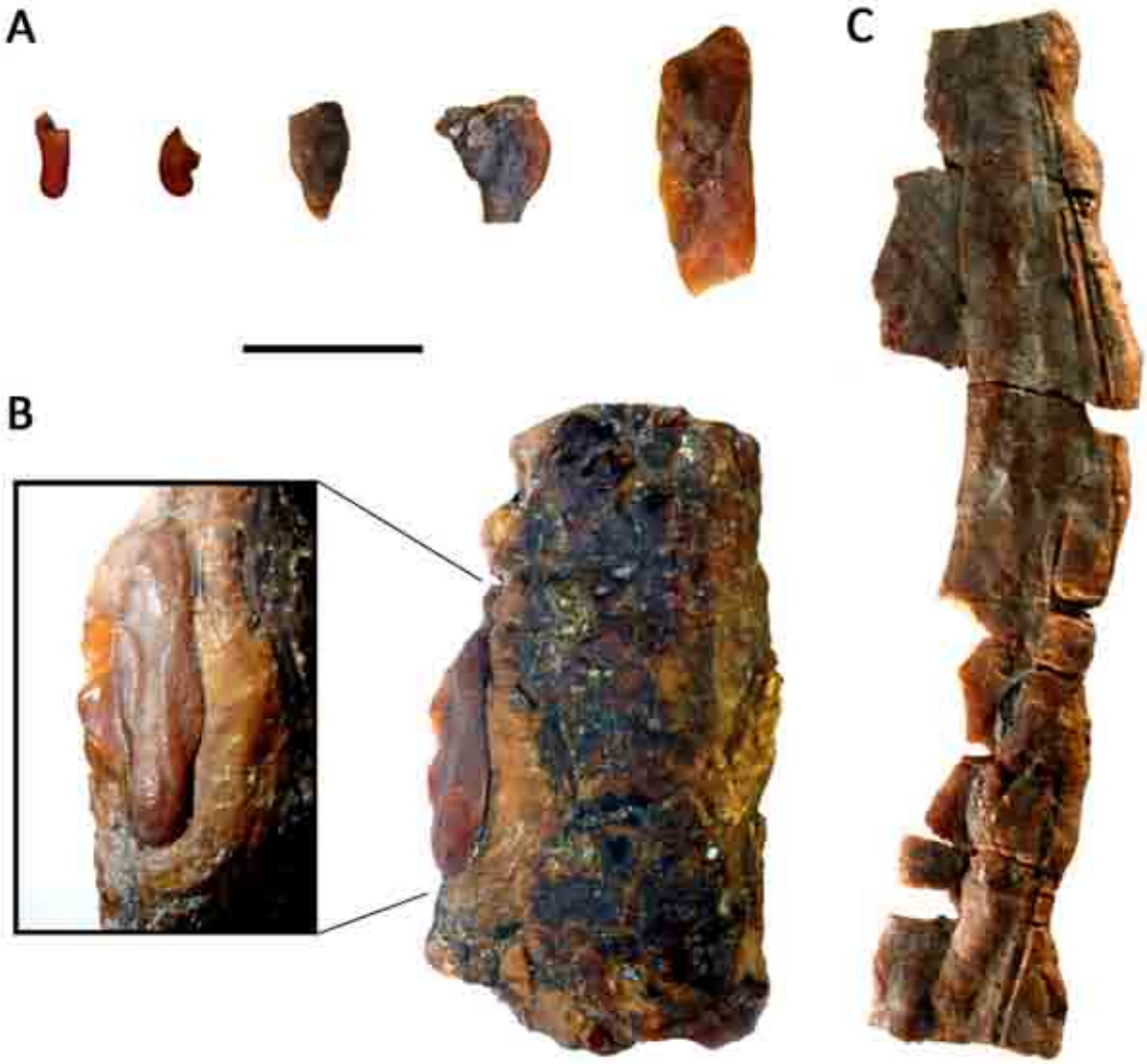
▲ **Tabla 2.** Familias de coníferas productoras de la resina que dio lugar al ámbar en los principales yacimientos del Cretácico. No existen fuentes que proporcionen el árbol productor del ámbar de Taimyr.

En el ámbar de El Soplao, los estudios paleoquimiotaxonómicos de Menor Salván et al. (2010) indican dos orígenes botánicos: el ámbar de tipo A y el ámbar de tipo B. El productor sugerido para el ámbar de tipo A fue una conífera queirolepidiácea, presumiblemente †*Frenelopsis* sp., debido a la coincidencia de ciertos biomarcadores tanto en el ámbar como en las cutículas de hojas de esta planta, halladas muy abundantemente en la roca que contiene el ámbar (véase el apartado 4.2.2). Otra evidencia en el mismo sentido es la presencia de varias piezas de ámbar con impresiones de tallos vegetativos de esta conífera (Fig. 20, véase el apartado 5.1.2.2). Por otra parte, algunas de estas piezas de ámbar de tipo A muestran una intensa fluorescencia azul bajo la luz solar (Fig. 18H; Najarro et al., 2010: fig. 3.4, anexo I.2).

Esta fluorescencia es resultado de la emisión fluorescente en el espectro visible de los compuestos 1,6-dimethyl-5-(3'-methylbutyl)-5,6,7,-tetrahydro naftaleno, hidrocarburos de la familia del azuleno y metilnaftalenos (Menor-Salván et al., 2009, 2010). El origen botánico del ámbar de tipo B de El Soplao aún no se ha podido determinar.

5.1.2.2. Lugar de producción de resina en la planta productora

En función de la parte de la planta en donde se ha secretado la resina, ésta adquiere diversas morfologías que tienen el potencial de conservarse en forma de ámbar (Langenheim, 1995). Se distinguen dos morfologías básicas de piezas de ámbar, las piezas de origen aéreo y las que tuvieron un origen confinado.



▲ **Fig. 20.** Diversidad de piezas de ámbar de origen aéreo del ámbar de El Soplao. **A.** Piezas de ámbar en forma de lágrima y otros flujos de pequeño tamaño (CES 287, 286, 279, 281 y 196, respectivamente). **B**. Pieza de ámbar en forma de colada, mostrando un flujo de resina ampliado, en visión lateral. **C.** Pieza grande de ámbar en forma de colada con impresiones de tallos de †*Frenelopsis* sp. La pieza se fragmentó en el momento de ser extraída del sedimento. B y C aún no tienen sigla CES asignada. Escala = 3 cm (todas las piezas a la misma escala). Fotografías en A por Rafael López del Valle.

Las piezas de origen aéreo se originaron por resina secretada en las ramas, la superficie externa del tronco o en raíces expuestas, y presentan un mayor potencial fosilífero (Martínez-Delclòs et al., 2004). El tamaño y morfología de estas piezas es muy variable, pero suele reflejar un flujo a favor de la gravedad después de que la resina fuera secretada. El ámbar de El Soplao se caracteriza por una gran abundancia de este tipo de piezas. Algunas morfologías comunes son las de gota, las de estalactita, las de tubo, las de colada o las de lámina (Figs 4, 20; Najarro et al., 2009: fig. 9A, B, anexo I.1).

Su tamaño suele ser pequeño, de unos pocos centímetros de longitud, aunque algunas pueden superar excepcionalmente los diez centímetros de longitud o incluso alcanzar los 20 centímetros (Fig. 20C). A consecuencia de esta exposición aérea, algunas piezas presentan un patrón de laminación interno que corresponde a sucesivas coladas de resina a diferentes intervalos de tiempo. Entre colada y colada, las superficies de exposición al medio atraparon a los organismos (véase el apartado A.10.1.2; Najarro et al., 2009: fig. 9C, anexo I.1).

Las piezas de ámbar de origen confinado se originaron por resina secretada internamente en los troncos o ramas, o por raíces no expuestas al exterior. Por ese motivo, tienden a ser muy poco o nada fosilíferas. En el ámbar de El Soplao, estas morfologías corresponden a piezas globulosas o aplastadas, a menudo con lobulaciones (Fig. 21; Najarro et al., 2009: fig. 9D, anexo I.1). Su tamaño máximo conocido es de unos 20 centímetros de longitud máxima por unos 10 centímetros de grueso (Fig. 21C)

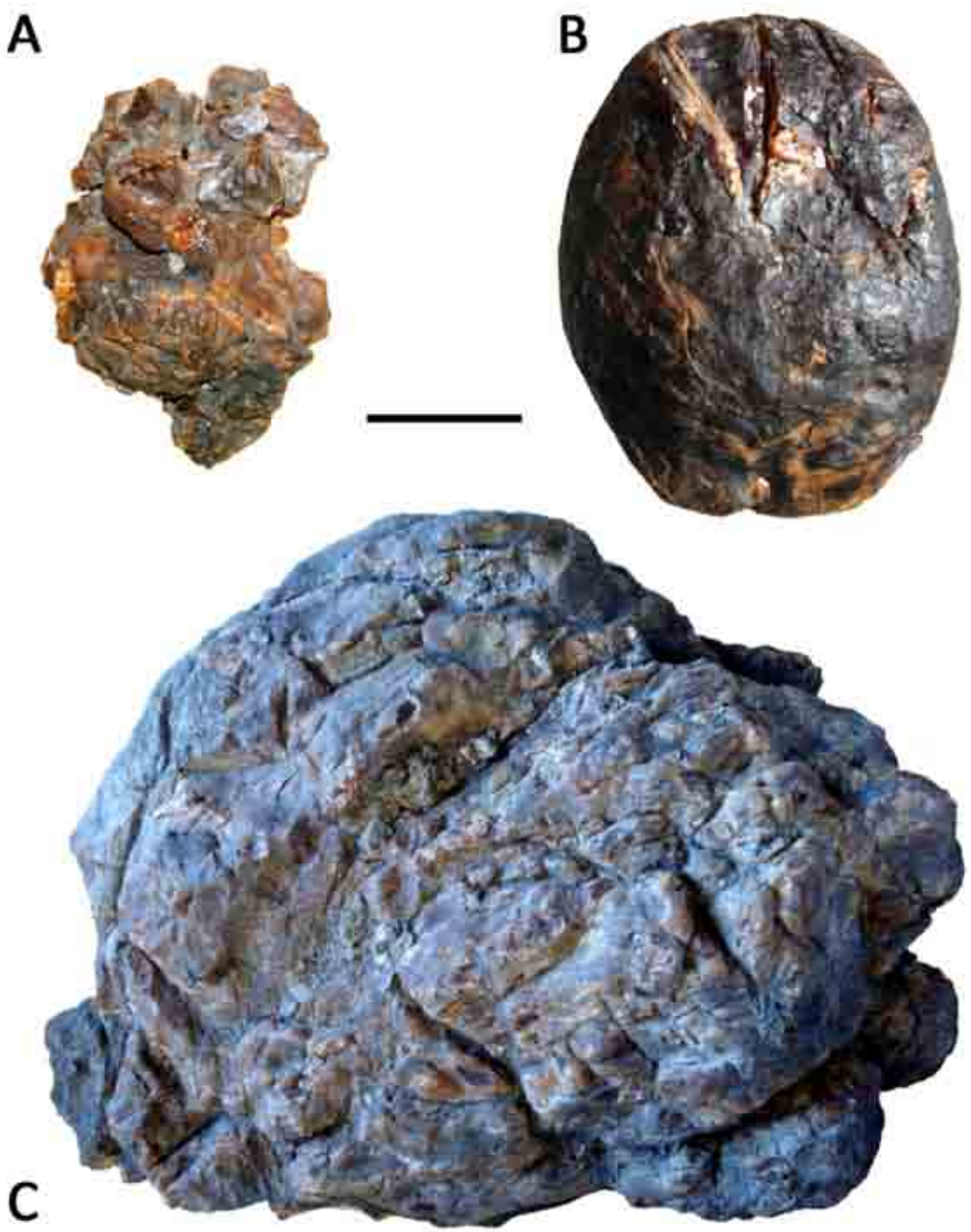
Cabe esperar un tercer grupo de piezas de ámbar sin morfología definida. Corresponde a aquella resina que hubiera caído al suelo por efecto de la gravedad, a menudo resbalando por las superficies de la planta productora. Este tipo de piezas puede llegar a preservar fauna edáfica (Perrichot, 2004).

5.2. Bioestratinomía: Transporte

El proceso de transporte de la resina se inicia en el suelo del bosque resinífero, en donde se encuentra acumulada, debido a procesos de erosión por el agua. Esta resina es transportada por el agua hasta que se deposita al disminuir la energía del flujo. Los típicos yacimientos de ámbar cretácico tienen su origen en el enterramiento de la resina transportada en sedimentos anóxicos en áreas de estuario-delta, asociados a una gran abundancia de restos de plantas (Martínez-Delclòs et al., 2004). La presencia en los yacimientos de estructuras frágiles de ámbar, como piezas con forma de estalactita o de gota, sugiere que el transporte no fue prolongado (ibid.).

5.3. Fosildiagénesis

El tiempo entre la secreción de la resina y su enterramiento es muy variable. La resina experimenta desde el momento de su secreción una pérdida de compuestos volátiles y una polimerización de los terpenoides y los compuestos fenólicos en un proceso de maduración



▲ **Fig. 21.** Piezas de ámbar de El Soplao con un origen en condiciones de confinamiento. **A.** Pieza de ámbar de forma arriñonada de 150 gramos de peso (CES 155). **B.** Pieza de ámbar de forma globulosa de alrededor de medio kilogramo de peso (CES 186). **C.** Pieza grande de ámbar globuloso con lobulaciones, de algo más de dos kilogramos de peso (CES 239). Escala = 5 cm (todas las piezas a la misma escala). Fotografías por Rafael López del Valle.

progresivo. Una vez que esta resina se entierra, este proceso continúa debido a las elevadas presiones y temperaturas (Langenheim, 2003). Aunque el criterio para determinar cuándo una resina se ha transformado en ámbar es laxo, se considera que una resina es ya fósil, y por tanto ámbar, a partir de alrededor de 40000 años de antigüedad (Anderson, 1996). Las resinas de menor edad, sin ser recientes, se consideran "subfósiles" y se conocen como copal.

Los tejidos orgánicos de los organismos incluidos en resina sufren una deshidratación y una carbonización desde muy temprano, de ahí que se considere que la fosildiagénesis de las inclusiones (en cierto sentido enterradas en resina) pueda empezar antes que la fosildiagénesis de la propia resina. Las propiedades antifúngicas y antibacterianas de la resina frenan o evitan los procesos de descomposición microbiana, aunque no evitan los procesos de autolisis ni el desarrollo de algunos tipos de hongos. Normalmente, las inclusiones de artrópodos en ámbar preservan tan sólo la cutícula, pero en algunos casos también se preservan tejidos internos blandos, como por ejemplo tejidos del sistema digestivo, nervioso y muscular (Soriano et al., 2010: anexo I.4). En un primer momento, la resina evita el colapso de los cuerpos de los organismos y por tanto mantiene su estructura tridimensional.

El ámbar es un material muy susceptible a la reelaboración, debido a su relativa resistencia a la meteorización y a que es fácilmente transportable por el agua (Martínez-Delclòs et al., 2004). De ahí que para datar correctamente el ámbar sea preciso conocer muy bien las características de enterramiento del yacimiento en el que aflora.

Los procesos diagenéticos principales que afectan a los depósitos de ámbar son la presión litostática y la temperatura elevada. Ello puede provocar la formación de fracturas en el ámbar (principalmente siguiendo los planos de las inclusiones), su oscurecimiento, o incluso su fusión, parcial o total (a 200-380^{o}C) (Martínez-Delclòs et al., 2004). Estos procesos anteriores también pueden afectar a las inclusiones, haciendo que su cutícula se deforme, o adquiera un aspecto oscurecido y a la vez semitransparente al permitir el paso de la luz (Rasnitsyn & Quicke, 2002). Aunque la preservación general de las bionclusiones del ámbar de El Soplao es buena, algunas bioinclusiones presentan este aspecto oscurecido y deformado, además de carecer de la película gaseosa de aspecto plateado que a menudo envuelve la cutícula y resalta los caracteres por reflejar intensamente la luz.

Por último, los procesos de meteorización son un agente destructor del ámbar cuando éste aflora, mediante la oxidación, la alteración debida a la luz ultravioleta y la formación de fracturas en el mismo.

6. SISTEMÁTICA Y PALEOBIOLOGÍA

6.1. Criterios de selección de los grupos estudiados

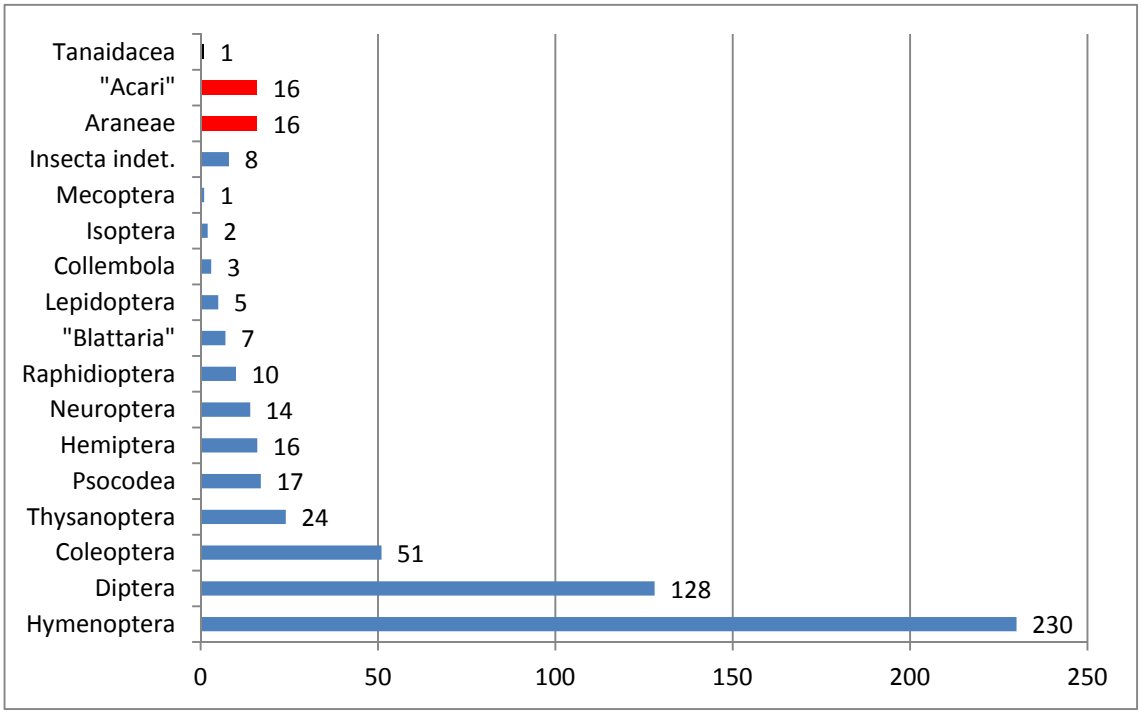
Los grupos de artrópodos que han sido directamente estudiados con motivo del presente Proyecto de Tesis Doctoral pertenecen a dos grupos principales, insectos y arácnidos. Respecto a los insectos, se han estudiado los rafidiópteros, neurópteros, himenópteros y dípteros. El grupo de arácnidos estudiado ha sido las arañas, si bien se han reconocido también varios grupos de ácaros. Otros miembros del equipo investigador han realizado otros estudios incluyendo material de El Soplao con tisanópteros e himenópteros (véanse los apartados A.6. y A.10.1.3.1; Nel et al., 2010; Ortega-Blanco et al., 2011a,b). Queda todavía mucho material de El Soplao por estudiar (anexo II), lo cual implicaría un tiempo de dedicación que supera enormemente el desarrollo de una Tesis Doctoral.

El criterio que ha determinado la prioridad de estudio de los ejemplares para la consecución de este Proyecto de Tesis Doctoral ha sido el de mayor potencial informativo a nivel paleobiológico. Bajo esta premisa, se ha dado preferencia al estudio de los neuroptéridos (aquí, neurópteros y rafidiópteros) y de arañas debido a que el estudio de ambos grupos en el ámbar de España había sido inexistente o marginal, pese haber ido apareciendo frecuentemente en las colecciones de Peñacerrada I y San Just (Delclòs et al., 2007; Peñalver & Delclòs, 2010). Ningún neuroptérido del ámbar de España había sido descrito o investigado hasta el presente Proyecto de Tesis Doctoral, mientras que sólo dos arañas habían sido descritas del ámbar de Peñacerrada I (Penney, 2006a; Penney & Ortuño, 2006). El estudio detallado de estos grupos ha sido sólo posible gracias a su buen registro, tanto en abundancia relativa como en preservación, ya desde el descubrimiento del yacimiento de El Soplao en 2008. Además, se ha dado prioridad de estudio a grupos que permitieran la comparación del ámbar de El Soplao con el resto de ámbares cretácicos españoles y mundiales.

En aquellos casos en los que se ha podido disponer de material adicional, el estudio de la paleofauna de artrópodos del yacimiento de El Soplao se ha llevado a cabo conjuntamente con ejemplares pertenecientes a otros yacimientos de ámbar coetáneos y próximos paleogeográficamente, ésto es, los yacimientos españoles de Peñacerrada I y San Just, y el yacimiento francés de Archingeay-Les Nouillers (todos de edad Albiense). Ello ha permitido contextualizar mejor los hallazgos de El Soplao y aumentar su potencial informativo mediante la comparación de los ejemplares. Además, en algunos casos (Pérez-de la Fuente et al., 2012a: anexo I.6) ha sido posible la comparación de taxones estudiados con los descritos de los yacimientos de compresión del Cretácico Inferior (Barremiense) de calizas litográficas de El Montsec en Lleida y las Hoyas en Cuenca, la fauna entomológica de los cuales es bien conocida (véase por ejemplo Whalley & Jarzembowski, 1985; Martínez-Delclòs 1989, 1991; Martínez-Delclòs & Nel, 1995).

6.2. Datos resumidos de abundancia

Un total de 549 macrobioinclusiones del ámbar de El Soplao pertenecientes a artrópodos han sido determinadas y catalogadas hasta la fecha. Corresponden a un total de 13 órdenes de hexápodos (con unas 40 familias determinadas), cuatro órdenes de arácnidos (arañas y tres órdenes de ácaros) y un orden de crustáceos (Fig. 22). El grupo más abundante de artrópodos es el de los himenópteros (41,9% del total de bioinclusiones de artrópodos), seguido por dípteros (23,3%) y luego coleópteros (9,2%). Estos tres grupos pueden considerarse como los grupos mayoritarios, conformando el 74,5% del total de bioinclusiones de artrópodos hallados en el yacimiento de El Soplao. El resto de grupos de artrópodos se consideran minoritarios en términos de abundancia relativa (representan menos del 5% del total de bioinclusiones de artrópodos), y son, por abundancia: tisanópteros, psocodeos, hemípteros, arañas, ácaros, neurópteros, rafidiópteros, blátidos, lepidópteros, colémbolos, isópteros, mecópteros y crustáceos tanaidáceos. Estos datos se discuten en el apartado 7.



▲ **Fig. 22.** Abundancia de bioinclusiones pertenecientes a los distintos grupos de artrópodos hallados en el ámbar de El Soplao. En azul, grupos de hexápodos; en rojo, grupos de arácnidos. En negro (arriba) se muestra el único grupo de crustáceos hallado.

El listado resumido de ejemplares hallados a nivel de familia (o superfamilia, en su defecto) de cada grupo de artrópodos se muestra en la Tabla 3. El listado detallado de todas las muestras catalogadas a fecha de julio de 2012 de El Soplao se muestra en el anexo II. Un resumen del material estudiado relacionado con el presente Proyecto de Tesis Doctoral (material publicado y por publicar) se muestra en el anexo III.

HEXAPODA		
HYMENOPTERA	Alavarommatidae?	1
	Aulacidae?/Gasteruptiidae?	1
	Bethylidae	1
	Braconidae	1
	Chrysididae?	1
	Evaniidae	4
	Maimetshidae	4(1?)
	Megalyridae	1
	Mymaridae?	1
	Mymarommatidae	5
	Serphitidae	4
	Platygastridae	91(2?)
	Stigmaphronidae	2
	Tiphiidae?	3
	Chrysidoidea indet.	2
	Mymarommatoidea indet.	1
	Vespoidea indet.	1
	Indet.	103
	TOTAL	**230**
DIPTERA	Atelestidae	3
	Cecidomyiidae	1
	Ceratopogonidae	43
	Chimeromyiidae	5
	Chironomidae	7
	Dolichopodidae	8
	Hybotidae	4
	Phoridae	9
	Psychodidae	4
	Rhagionidae	3
	Zhangsolvidae	5*
	Psychodoidea indet.	1
	Brachycera indet.	17
	"Nematocera" indet.	8
	Diptera indet.	10
	TOTAL	**128**
COLEOPTERA	Carabidae?	2
	Cleridae	2
	Dermestidae?	2
	Latridiidae	3
	Scraptiidae	1
	Staphylinidae	4
	Curculionoidea indet.	2
	Elateroidea indet.	4
	Indet.	31
	TOTAL	**51**
THYSANOPTERA	Thripidae	1
	Indet.	23
	TOTAL	**24**
PSOCODEA	Psocoptera Indet.	**17**
HEMIPTERA	Aleyrodidae	3
	Psylloidea indet.	1
	Fulgoroidea indet.	1
	Sternorrhyncha indet.	5
	Heteroptera indet.	4
	Indet.	1(1?)
	TOTAL	**16**
NEUROPTERA	Berothidae	3
	Coniopterygidae	7
	Psychopsidae	1
	Nymphidae?	1
	Chrysopoidea indet.	1
	Indet.	1
	TOTAL	**14**
RAPHIDIOPTERA	**Mesoraphidiidae**	8
	Indet.	2?
	TOTAL	**10**
"BLATTARIA"	Indet.	**6(1?)**
LEPIDOPTERA	Micropterygidae	1
	Indet.	3(1?)
	TOTAL	**5**
COLLEMBOLA	Indet.	**3**
ISOPTERA	Indet.	**1(1?)**
MECOPTERA	Indet.	**1**
INSECTA INDET.	-	**8**
ARACHNIDA		
ARANEAE	Araneidae?	2
	Lagonomegopidae	2
	Oonopidae	1
	Indet.	11
	TOTAL	**16**
"ACARI"	Argasidae	1
	Bdellidae	1
	Erythraeidae	3
	Neoliodidae	1
	Nothridae	1
	Trhypochthoniidae	1
	Oribatida indet.	1
	Trombidiformes?	1
	Indet.	6
	TOTAL	**16**
CRUSTACEA		
TANAIDACEA	Indet.	1
.....	TOTAL INCLUSIONES	**549**

▲ **Tabla 3.** Listado de familias (o superfamilias en su defecto) y número de ejemplares existentes de los distintos grupos de artrópodos hallados en el ámbar de El Soplao. Los órdenes de hexápodos se listan en orden de abundancia relativa, mientras que las familias o superfamilias se muestran por orden alfabético, respectivamente. Aquellas familias (o superfamilias en su defecto) que han sido motivo de publicación de artículos (véase el anexo I) se muestran en rojo. *Estas cinco inclusiones corresponden a tres individuos (véase el apartado A.12.2.1).

6.3. Paleobiodiversidad detallada de artrópodos

A continuación se exponen los distintos grupos de artrópodos que conforman la diversidad del ámbar de El Soplao. El orden de aparición de los distintos grupos de hexápodos ha venido determinado por un criterio evolutivo, tal y como se sigue en la obra "*Evolution of the Insects*" de Grimaldi & Engel (2005). Los grupos de artrópodos que han sido motivo de publicación por parte del doctorando se han indicado haciendo constar el apartado del anexo I en el que se presenta su publicación. La información que se muestra aquí de ellos sirve de resumen de los resultados obtenidos en sus respectivas publicaciones remitidas al anexo. Cabe destacar que, si bien los trabajos relativos a arañas palpimanoideas (excluyendo a los lagonomegópidos, ya publicados) y neurópteros, pese a hallarse en un estado avanzado de confección y haber conllevado un volumen de trabajo sustancial en este proyecto de Tesis Doctoral, no han entrado en fase de publicación aún, de ahí que se hayan ampliado en el anexo IV y V, respectivamente.

Una parte de las determinaciones taxonómicas del material de El Soplao que aquí se exponen, relativas a material no publicado, ha sido llevada a cabo junto con otros miembros del equipo investigador del proyecto AMBARES (acrónimo de ÁMBARes de ESpaña). Las determinaciones taxonómicas relativas a coleópteros han sido llevadas a cabo por el Sr. David Cerdán, de la Universitat de Barcelona, que actualmente está desarrollando su Tesis Doctoral sobre los coleópteros del ámbar de España. La mayor parte de determinaciones taxonómicas de himenópteros a nivel familiar (exceptuando el grupo de los esceliónidos) ha sido realizada por los doctores Jaime Ortega Blanco y Michael Engel, de la University of Kansas. Finalmente, los dípteros braquíceros a niveles de familia o de género y los ácaros a nivel de orden han sido determinados por el Dr. Antonio Arillo, de la Universidad Complutense de Madrid. Además, el Dr. Luis Subías ha colaborado en la determinación de los ácaros.

6.3.1. = A. SUBFILO HEXAPODA

A.1. O. COLLEMBOLA

Los colémbolos, hexápodos no insectos con unas 8000 especies actuales conocidas (Bellinger et al., 2012), presentan una gran variedad de modos de vida, siendo micófagos, detritívoros, fitófagos o depredadores, y son típicamente habitantes del suelo aunque también viven en otros sustratos como los árboles (Hopkin, 1997). Si bien la historia evolutiva de los colémbolos se remonta hasta el Devónico Inferior, existe un gran vacío en su registro fósil hasta que reaparecen en los ámbares del Cretácico Inferior (Grimaldi & Engel, 2005). De este periodo, existen sólo colémbolos descritos de los ámbares de España (Peñacerrada I) y Canadá (Christiansen & Pike, 2002; Simón-Benito et al., 2002), aunque han sido también hallados en los ámbares del Líbano, Myanmar, Francia (Archingeay-Les Nouillers) y Federación de Rusia (Taimyr) (Azar, 2000; Grimaldi et al., 2002; Perrichot et al., 2007). Los colémbolos son raros en el ámbar de El Soplao, contándose sólo con tres especímenes descubiertos hasta la fecha (CES 530.19 + 530.23 + 530.24). Todos ellos son sininclusiones en una pieza excepcional con 24 artrópodos reconocidos (Fig. 7).

A.2. O. "BLATTARIA"

El orden de las cucarachas, con unas 4000 especies actuales, representa una agrupación parafilética, puesto que para ser monofilética debería incluir al orden de las termitas (Grimaldi & Engel, 2005). Se trata de insectos hemimetábolos (de metamorfosis incompleta), cosmopolitas y presentes en todo tipo de hábitats, siendo herbívoros, detritívoros o depredadores, y en algunos casos polífagos (Bell et al., 2007). Se conocen desde el Carbonífero Superior, estando desde entonces siempre muy presentes en los yacimientos de compresión/impresión paleozoicos y mesozoicos (ibid.). En España están bien presentes en los registros cretácicos del Montsec y Las Hoyas (Barremiense Inferior) (Martínez-Delclòs, 1993; Vršanský & Ansorge, 2001). Las cucarachas son mucho menos frecuentes en los yacimientos cretácicos de ámbar, tratándose la mayoría de juveniles debido al sesgo tafonómico que se da en los yacimientos de ámbar a favor de la conservación de individuos de pequeño tamaño (Vršanský, 2009). Se han descrito algunos taxones de los ámbares del Líbano, Myanmar y EUA (Nueva Jersey) (Vršanský, 2004; Grimaldi & Ross, 2004; Anisyutkin & Gorochov, 2008), pero la fauna mejor estudiada es la del ámbar de Archingeay-Les Nouillers (Vršanský, 2009). Aunque este grupo ha sido hallado en los ámbares de Peñacerrada I, San Just y La Hoya, ningún ejemplar ha sido descrito hasta la fecha. En El Soplao se han hallado siete ejemplares de cucarachas (CES 056.3, 130.8, 413.5, 426.2, 473, 517 y 526.1), algunas de ellas juveniles (Fig. 23A; Najarro et al., 2009: fig. 12D, anexo I.1).

▲ **Fig. 23.** **A**. Cucaracha inmadura, CES 130.8 ("Blattaria"). **B**. Psocóptero, CES 465 (Psocodea). Escalas: A = 2 mm; B = 0,5 mm.

A.3. O. ISOPTERA

El orden de los isópteros, o termitas, corresponde a un linaje monofilético que se escindió de las cucarachas en el Jurásico Superior, presentando sus primeros registros en el Cretácico Inferior (Engel et al., 2009a). Se trata, con alrededor de 2500 especies y una distribución cosmopolita, del grupo de insectos eusociales más antiguo que existe (Bignell et al., 2010), existiendo registro de esta eusociabilidad desde el Barremiense del Montsec (Martínez-Delclòs & Martinell, 1995). La colonia vive en nidos excavados bajo tierra o en la

madera de la que se alimentan, o bien construye nidos en los árboles o montículos usando sus regurgitaciones y heces. Las termitas se alimentan de todo tipo de materia vegetal, en diversos estados de descomposición y humidificación según el grupo, aunque algunas termitas cultivan hongos a partir de esta materia vegetal (ibid.). Como ocurre en los yacimientos cretácicos (ibid.), la abundancia relativa de este grupo es muy escasa también en El Soplao, existiendo tan sólo un ejemplar (CES 552) y otro dudoso (CES 446.1). Tres géneros y tres especies de termitas han sido descritos del ámbar de España, dos de Peñacerrada I y uno de San Just (Engel & Delclòs, 2010). Estas termitas ocupan un grado filogenético indefinido entre los primitivos mastotermítidos (con un representante vivo australiano que preserva claras características morfológicos de su relación con las cucarachas) y las familias basales Termopsidae, Hodotermitidae, Archotermopsidae y Stolotermitidae (ibid.). Además, se han descrito termitas del Líbano, Myanmar y EUA (Nueva Jersey) (Engel et al., 2009a).

A.4. O. PSOCODEA

Este orden de insectos hemimetábolos (superorden para algunos autores) alberga los antiguos órdenes de los psocópteros (=Psocoptera) y los piojos (=Phthiraptera). Los psocópteros, con unas 5500 especies actuales, son insectos hemimetábolos cosmopolitas de hábitats muy variados aunque típicamente asociados a vegetación, que se alimentan básicamente de microflora epifítica y detritus, aunque existen casos de depredación (New & Lienhard, 2007). Los primeros fósiles atribuibles en sentido estricto a este grupo se hallan en el Jurásico Superior, siendo habituales en los principales ámbares cretácicos (Grimaldi & Engel, 2005). Este orden es relativamente habitual en los ámbares españoles, de cuyo registro se han descrito ejemplares pertenecientes a sus tres subórdenes: Trogiomorpha, Troctomorpha y Psocomorpha. Aunque el ámbar de El Soplao cuenta con 17 especímenes de psocópteros (Fig. 23B), su estudio todavía no se ha iniciado. En el ámbar de Peñacerrada I se describieron cuatro especies dentro del suborden Trogiomorpha, tres especies pertenecientes a la familia Empheriidae Enderlein, 1906 y una especie de la nueva familia †Archaeatropidae Baz & Ortuño, 2000 (Baz & Ortuño, 2000; Baz & Ortuño, 2001a). Asimismo, dentro del suborden Troctomorpha se describió una nueva especie asignada tentativamente a la familia Manicapsocidae Mockford, 1967 (Baz & Ortuño, 2001b). Además, se han descrito psocópteros diversos de los ámbares cretácicos del Líbano, Myanmar, Francia (Archingeay-Les Nouillers), EUA (Nueva Jersey), Federación de Rusia (Taimyr) y Canadá (e.g., Perrichot et al., 2003; Grimaldi & Engel, 2006; Azar et al., 2009; Azar et al., 2010b,c; Azar & Nel, 2011; Choufani et al., 2011).

A.5. O. HEMIPTERA

Los hemípteros, con unas 90000 especies conocidas, son el orden de insectos hemimetábolos más diverso que existe, con registro desde el Pérmico (Grimaldi & Engel,

2005). En El Soplao se han reconocido representantes de los tres subórdenes principales de hemípteros, esto es, Sternorrhyncha, Auchenorrhyncha y Heteroptera. Mientras que todos los miembros de Sternorrhyncha y Auchenorrhyncha pueden considerarse fitófagos, los heterópteros son depredadores a nivel evolutivamente basal, si bien algunos de sus grupos han revertido a la fitofagia secundariamente (ibid.). El suborden Sternorrhyncha es el más abundante, y se halla representado por, al menos, las familias Aleyrodidae (CES 060, 429 y 530.3) y la superfamilia Psylloidea (CES 351). Mientras que la primera está bien representada en los ámbares cretácicos (véase Drohojowska & Szwedo, 2011), los psiloideos tienen un registro muy pobre (Ouvrard et al., 2010). Por otra parte, ya dentro de Auchenorrhyncha, se ha reconocido un fulgoroideo (CES 055, Fig. 24). Respecto a los heterópteros, se han hallado tres ejemplares juveniles (CES 010.1 + 010.2 + 010.3) y un adulto (CES 507).

▲ **Fig. 24.** Fulgoroideo (Hemiptera: Auchenorrhyncha) del ámbar de El Soplao, CES 055. Escala = 1 mm.

A.6. O. THYSANOPTERA: F. Thripidae Stevens, 1829

Los tisanópteros, o trips, son pequeños insectos hemimetábolos de distribución mundial con alrededor de 6000 especies descritas (Mound, 2007). Al contrario de lo que clásicamente se creía, se ha demostrado que actualmente juegan un importante papel como polinizadores, tanto de gimnospermas como de angiospermas, hecho que también se ha constatado que ocurría en el Cretácico en relación con las gimnospermas (Peñalver et al.,

2012). Aproximadamente, un tercio del total de especies actuales de trips descritas corresponde a la familia Thripidae. Se alimentan perforando con su aparato bucal de tipo picador estructuras mayoritariamente de origen vegetal, como polen o células, o más raramente de origen animal, absorbiendo el contenido líquido (Mound, 2005). Se ha descrito una nueva especie de trípido del ámbar de El Soplao, *Tethysthrips hispanicus* Nel, Peñalver, Azar, Hodebert & Nel, 2010 (CES 451) (Najarro et al., 2009: fig. 12a, anexo I.1; Nel et al., 2010). Representa la especie tipo del género †*Tethysthrips*, en el que también se clasifica *T. libanicus* Nel, Peñalver, Azar, Hodebert & Nel, 2010, del ámbar del Líbano. Además de los ámbares del Líbano y España, la familia está presente en los ámbares cretácicos de Myanmar, Federación de Rusia (Taimyr) y Canadá, y adquiere predominancia en los ámbares cenozoicos de Francia y el Báltico (Zherikhin, 2002; McKellar et al., 2010; Ross et al., 2010).

A.7. O. RAPHIDIOPTERA: F. †Mesoraphidiidae Martynov, 1925 - Pérez-de la Fuente et al. (2010) y Pérez-de la Fuente et al. (2012a): anexo I.3 y anexo I.6

Los rafidiópteros son los insectos holometábolos (de metamorfosis completa) más primitivos que existen, hecho que se manifiesta por la singularidad de tener una fase pupal móvil y activa (Aspöck, 2002; Grimaldi & Engel, 2005). Tanto sus fases inmaduras como su fase adulta son depredadoras, esta última reconocible por un largo cuello y un largo ovipositor en las hembras, hecho que les ha conferido su nombre vulgar de moscas serpiente. Aunque su distribución actual se restringe a climas fríos del Hemisferio Norte, su registro fósil revela un pasado más diverso, ya que el grupo habitó en climas subtropicales y tropicales también del Hemisferio Sur (Aspöck et al., 1991). Este registro fósil corresponde mayoritariamente a la familia †Mesoraphidiidae, muy extendida en el Hemisferio Norte desde el Jurásico Superior hasta el Cretácico Superior, con unas 60 especies descritas hasta ahora clasificadas en 24 géneros, la mayoría de ellas procedentes de yacimientos de compresión-impresión. Inesperadamente, el registro de este grupo en el ámbar de España en general, y en el de El Soplao en particular, se ha revelado muy abundante si se compara con el registro del grupo en los otros yacimientos de ámbar cretácico. Ello se manifiesta con tres nuevos géneros y especies descritos del ámbar de El Soplao: *Cantabroraphidia marcanoi* Pérez-de la Fuente, Nel, Peñalver & Delclòs, 2010 (ES-07-06), *Necroraphidia arcuata* Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012 (CES 391.1) y *Amarantoraphidia ventolina* Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012 (CES 364.1). Cabe añadir un resto parcial descrito (CES 376), y cuatro nuevas inclusiones recientemente descubiertas (CES 590, 595 y 597.1 + 597.2). Completan la diversidad recientemente descrita del ámbar de España nuevos morfotipos descritos como un nuevo género y especie, y dos nuevas especies del ámbar de Peñacerrada I, incluido el primer baisoptérido en ámbar, así como dos restos indeterminados (véase el anexo III).

Los otros ámbares cretácicos, del Líbano, Myanmar, Francia, EUA (Nueva Jersey) y Canadá, han proporcionado hasta la fecha registros muy escasos de rafidiópteros adultos. Especialmente sorprendente es que los yacimientos franceses, pese a su cercanía geográfica y sus edades relativamente similares, no hayan brindado ningún resto de rafidióptero, a excepción de dos restos larvarios del ámbar de Archingeay-Les Nouillers (Perrichot & Engel, 2007). Una hipótesis para explicar la especial diversidad y abundancia relativa de este grupo en

el ámbar de España es que ello esté reflejando una peculiaridad paleofaunística de la Placa Ibérica durante el Cretácico Inferior fruto de su aislamiento geográfico desde el Jurásico Superior (véase Blakey, 2011). Sin embargo, otra hipótesis complementaria está relacionada con el predominante rol que los paleoincendios hubieran podido desempeñar en el ecosistema boscoso ibérico durante el Cretácico Inferior. Ello, aunque se ha considerado que pudo ser un fenómeno generalizado (Brown et al., 2010), tan sólo ha sido demostrado a partir del registro de los yacimientos españoles (Najarro et al., 2010: anexo I.2) y el del ámbar de Nueva Jersey (Grimaldi, 2000). Los incendios, como fenómeno integrante de la dinámica del paleoecosistema, habrían incrementado de modo recurrente la disponibilidad de madera muerta como sustrato para el desarrollo de los insectos xilófagos o xilófilos. Este hecho habría permitido el incremento de las poblaciones xilófilas de mesorafídidos. En efecto, lo más probable es que los mesorafídidos hubieran tenido una biología ligada a la madera de los árboles, tal y como sucede en muchos rafidiópteros actuales (Aspöck, 2002). Ello está en consonancia con la constatación en el registro de ámbar cretácico de una cierta abundancia relativa de larvas de mesorafídido en comparación con el registro de larvas del resto de insectos holometábolos. Los estudios del ámbar de El Soplao aportan evidencias que inciden en esta posibilidad, por ejemplo el hallazgo de abundantes fragmentos de madera como sininclusiones junto a los holotipos de *C*. *marcanoi*, *N*. *arcuata* y *A*. *ventolina*, los dos últimos con presencia adicional de fragmentos de fusinita. Además, la buena preservación de los ejemplares completos, siendo uno de ellos *A. ventolina*, ha permitido reconocer que su ovipositor presenta anulaciones, hecho que actualmente representa una adaptación para que las rafídias hembra puedan flexionar el ovipositor e introducirlo entre las oquedades de la madera (Mickoleit, 1973).

A.8. O. NEUROPTERA

Este orden de primitivos holometábolos, con unas 6000 especies descritas, cuenta con registro fósil desde el Pérmico Inferior (Haring & Aspöck, 2004; Shcherbakov et al., 2009). Una característica común a todos sus miembros es que las larvas presentan piezas bucales formadas por la unión de maxilas y mandíbulas, las cuales se usan a modo de jeringuillas para succionar los fluidos vitales de sus fuentes de alimentación, normalmente otros insectos (Grimaldi & Engel, 2005).

A.8.1. Subo. Myrmeleontiformia

A.8.1.1. Superf. Myrmeleontoidea: F. Nymphidae? Rambur, 1842 - Anexo V

Se ha hallado una inclusión parcial de un neuróptero de gran tamaño (CES 477), correspondiente a las mitades basales de un ala anterior y otra posterior del mismo lado del cuerpo, así como porciones de tórax y abdomen. Este fragmento se considera, de forma tentativa, dentro de la familia Nymphidae Rambur, 1842, ya que por la ausencia de caracteres diagnóstico pudiera también corresponder a otros grupos de neurópteros con un patrón alar basal similar, como algunos miembros de la familia Osmylidae Leach, 1815.

A.8.1.2. Superf. Nemopteroidea: F. Psychopsidae Handlirsch 1906 - Anexo V

Los psicópsidos, con alrededor de una treintena de especies conocidas, conforman una pequeña familia de neurópteros con una diversidad y distribución relictas (Grimaldi & Engel, 2005). Se conocen unas 35 especies fósiles, en su gran mayoría correspondientes a restos de compresión (Peng et al., 2011). Un magnífico individuo completo de gran tamaño, alrededor del centímetro de longitud (CES 390.1), se ha identificado dentro de esta familia, correspondiendo a un morfotipo que podrá ser descrito como nuevo género y especie. El nuevo morfotipo representa, a fecha de hoy, el único fósil de un individuo completo del Cretácico asignable a la familia.

A.8.2. Subo. Hemerobiiformia

A.8.2.1. Superf. Chrysopoidea - Pérez-de la Fuente et al. (2012e, *reenviado a la revista tras informe favorable de revisores*): anexo I.11

Uno de los hallazgos más singulares que ha brindado el ámbar de El Soplao es un ejemplar larvario emparentado con los actuales crisópidos, familia Chrysopidae Hagen, 1866, actualmente con unas 1500 especies de distribución mundial (Grimaldi & Engel, 2005). Las larvas de crisópido son voraces depredadores de varios milímetros de tamaño corporal muy utilizadas en el control de plagas en el cultivo, de ahí que hayan sido ampliamente estudiadas a nivel ecológico (Canard et al., 1984). Estos neurópteros inmaduros usan sus características piezas bucales en forma de hoz a modo de jeringuillas, con las que licúan y absorben las sustancias internas de sus presas (ibid.). El *trash-carrying* (o transporte de basura) es un hábito de algunas larvas de crisópido consistente en la selección, carga y transporte de diverso material orgánico con la finalidad de camuflarse, ante sus presas y depredadores, y protegerse (Eisner et al., 1978). Para confeccionar su *trash packet* (o paquete de basura), la larva busca activamente un tipo o varios de restos de origen vegetal (trozos de madera, fibras vegetales, tricomas...) y/o animal (cadáveres de presas, exuvias, secreciones cerosas de pulgones...), y los carga sobre su dorso mediante movimientos hacia atrás de la cabeza y la adopción de ciertas posturas corporales (Jones, 1941). La protección que el paquete defensivo brinda contra los depredadores actúa a dos niveles. Por una parte, evita que la larva sea reconocida por los atacantes, bien sea proporcionando camuflaje visual o engañando a los atacantes por reconocimiento erróneo por contacto (Eisner et al., 1978; Eisner & Silberglied, 1988). En segundo lugar, el *trash packet* actúa de escudo físico ante depredadores y parásitos (Eisner et al., 2002). En algunos casos, la larva puede incluso enrollarse sobre sí misma para que el paquete de basura la envuelva completamente y así hacer frente a varios atacantes simultáneamente (Eisner & Eisner, 2002). El paquete de basura es algo tan fundamental para la biología de la larva que su reparación o reconstrucción tiene prioridad ante la alimentación (Anderson et al., 2003). Como adaptación morfológica al *trash-carrying*, las larvas de crisópido muestran ciertas estructuras especializadas. Se trata de adaptaciones que aumentan el potencial de retención de los elementos del paquete de basura, y generan además un mayor espacio donde poder transportarlos. Relacionado con esta adaptación, el abdomen de la larva puede ser abombado y presentar los dorsos del tórax y del abdomen densamente recubiertos con setas, a menudo con setas que presentan especializaciones tales como denticiones,

espinas o extremos en forma de gancho (McEwen et al., 2001). Asimismo, los segmentos torácicos y abdominales de la larva pueden mostrar pares de tubérculos dorsales, con una longitud variable menor que la de la cápsula cefálica, provistos de largas setas que también pueden presentar las especializaciones antes mencionadas.

El fósil de El Soplao (CES 418), descrito como un nuevo género y especie, corresponde a una larva afín a los actuales crisópidos, la cual muestra preservado un paquete de basura. Este paquete de basura se halla compuesto por tricomas con afinidad a un grupo de helechos (véase abajo). El registro previo de inmaduros de crisópido, hallado exclusivamente en ámbar, es sumamente escaso, limitándose a un neonato (Canadá) y tres larvas (dos del Báltico y una de República Dominicana) (Hagen, 1856; Engel & Grimaldi, 2007, 2008; Weitschat, 2009). De todos ellos, sólo una de las dos larvas del Báltico preservó su paquete de basura (Weitschat, 2009). El ejemplar de El Soplao no se ha asignado a ninguna familia dentro de la superfamilia Chrysopoidea debido a su disparidad morfológica con las actuales larvas de crisópido y a que existe consenso en considerar que Chrysopidae *sensu stricto* se originó con posterioridad al límite K/T (Nel et al., 2005). Por tanto, lo más plausible es que la larva corresponda a un inmaduro de alguna de las familias fósiles de crisopoideos que han sido descritas a partir de ejemplares adultos, algunos de ellos hallados en los yacimientos de Las Hoyas o El Montsec (ibid.), pero la relación con una familia concreta no es posible. La característica morfológica más sorprendente del fósil es que presenta unos tubérculos dorsales extremadamente alargados, presentando morfología tubular y disposición radial, siendo algunos más largos incluso que el cuerpo de la larva. Asimismo, las setas de estos tubérculos dorsales poseen una especialización única, ya que sus terminaciones están expandidas en forma de trompeta (Pérez-de la Fuente et al., 2012e, *reenviado a la revista tras informe favorable de revisores*: fig. S1, anexo I.11). Ello hubiera actuado a modo de ancla entre las marañas de tricomas, especialmente cuando las setas se hubieran doblado por el peso del paquete de basura. Este sistema de cohesión de los elementos del *trash-packet* es desconocido en Chrysopidae, pero se halla presente en algunas larvas de los neurópteros de la familia Nymphidae Rambur, 1842 (New, 1982). Tras contextualizar el hallazgo en el marco del resto de invertebrados conocidos que presentan hábitos de camuflaje mediante la selección activa y transporte de material exógeno, como erizos de mar, arañas, cangrejos decoradores o insectos inmaduros como chinches redúvidas o coleópteros crisomélidos (Pérez-de la Fuente et al., 2012e *reenviado a la revista tras informe favorable de revisores*: fig. 4, anexo I.11; Berke et al., 2006), se pone de manifiesto cómo el nuevo fósil representa uno de las evidencias directas más antiguas conocidas de camuflaje en el registro fósil, no sólo entre los insectos, sino también entre invertebrados en general.

Los tricomas son estructuras con una plasticidad morfofuncional extrema, por lo que se pueden usar para la caracterización taxonómica de los diversos grupos de plantas que los presentan (Uphof et al., 1962; Fahn, 1990). La morfología de los tricomas estudiados corresponde a un eje principal polarizado (ésto es, presentando una base de inserción) con ramificaciones secundarias alternantes y dispuestas en un sólo plano (Pérez-de la Fuente et al., 2012e *reenviado a la revista tras informe favorable de revisores*: figs 3, S3, anexo I.11). Se han reconocido dos tipos estructurales básicos de tricoma, que representan diferentes estadios de desarrollo. En uno de estos tipos (tipo II), el eje principal del tricoma presenta un

patrón flexuoso (en zig-zag) en el que las ramificaciones secundarias se dirigen hacia el ápice del tricoma. Además, los tricomas presentan una superficie ornamentada a base de micropapillas que muestran una fluorescencia azulada tras excitación con el ultravioleta, típica de compuestos fenólicos de la pared celulósica (Pfündel et al., 2007). Tras su comparación con tricomas de diversos grupos de plantas, preferentemente aquellos grupos de plantas aparecidos en El Soplao, tanto por el registro de macro y mesorrestos como palinológico (apartados 4.2.1. y 4.2.2; Najarro et al., 2009, 2010: anexos I.1 y I.2), la conclusión es que lo más plausible es que los tricomas que conforman el paquete de basura estén relacionados la familia tropical de helechos Gleicheniaceae, bien establecida y con amplia distribución durante el Cretácico (Bolchovitina, 1966; Skog, 2001). Estos helechos se hallan representados en El Soplao por las especies de esporas *Gleicheniidites senonicus* Ross, 1949 y *Ornamentifera peregrina* (Bolchovitina, 1953) Bolchovitina, 1968. Las gleicheniáceas actualmente suelen ser pioneras en la sucesión primaria tras eventos destructivos como incendios (Gillison, 1969; Russell et al., 1998). Su registro desde el Jurásico Superior corresponde típicamente a restos carbonizados o fusinizados, sugiriendo que ya en ese periodo eran plantas adaptadas a colonizar áreas arrasadas por incendios (Collinson, 2002; Van Konijnenburg-Van Cittert, 2002). Es por ello que la presencia de este grupo de helechos en El Soplao se ha vinculado a las abundantes evidencias de paleoincendios en el mismo (Najarro et al., 2010: anexo I.2).

Por todo lo expuesto, a partir de este registro excepcional, se concluye que el comportamiento del *trash-carrying* en las larvas de crisopoideo existía ya durante el Cretácico Inferior y ha permanecido en estasis durante 110 millones de años. Por otra parte, la monoespecificidad del paquete de basura sugiere que la larva de crisopoideo se alimentaba de insectos que vivían en el helecho. Ello implica la existencia una relación planta-insecto en la que las estructuras defensivas generadas por la planta para defenderse de los herbívoros son usadas por un insecto depredador para protegerse a sí mismo.

A.8.2.2. Superf. Coniopterygoidea: F. Coniopterygidae Burmeister, 1839 - Anexo V

Los coniopterígidos, con alrededor de 500 especies actuales conocidas repartidas a nivel mundial, son los neurópteros de menor tamaño, con un patrón alar simplificado y hábitos depredadores tanto en las larvas como en los adultos, si bien estos últimos pueden alimentarse también de materia vegetal (Grimaldi & Engel, 2005). Su registro fósil, conocido desde el Jurásico de Kazajistán (Meinander, 1975), está constituido por 13 especies mesozoicas y 14 especies cenozoicas, la gran mayoría descritas como inclusiones en ámbar (Anexo V: Tabla 1). De entre los coniopterígidos aparecidos en El Soplao, un total de siete, se ha reconocido la existencia de una nueva especie dentro del género *Glaesoconis* Meinander, 1975 (CES 348).

A.8.2.3. Superf. Mantispoidea: F. Berothidae Handlirsch, 1906 - Anexo V

Los berótidos (tratados aquí considerando a los rhachiberótidos como una familia aparte) conforman una pequeña familia de neurópteros con aproximadamente unas 115 especies actuales repartidas a nivel mundial (Engel & Grimaldi, 2008). Sus larvas han sido halladas en detritus tales como madera en descomposición y, más singularmente, en nidos de termitas cuando son depredadores obligados de éstas (Tauber & Tauber, 1968). Los hábitos

conocidos para los adultos indican una dieta polinívora o polífaga, cuando además de polen también se alimentan de insectos y/o néctar (véase por ej. Monserrat, 2006). Su registro fósil, de alrededor de una veintena de especies, se conoce desde el Cretácico, y procede de los ámbares del Líbano, Myanmar, EUA (Nueva Jersey) y Canadá, además de algunas localidades de compresión (véase Makarkin et al., 2011). En El Soplao, la familia está representada por un espécimen completo que corresponde a un nuevo morfotipo que podrá describirse como nuevo género y especie (CES 004; Najarro et al., 2010: fig. 8.4, anexo I.2), además de un ejemplar parcial (CES 014) que se considera un posible registro del género *Ethiroberotha* Engel & Grimaldi, 2008, descrito del ámbar de Myanmar. Un tercer ejemplar (CES 402.1) podría corresponder a este grupo.

A.9. O. COLEOPTERA

El registro de este orden tan diverso, con alrededor de 350000 especies actuales descritas, se conoce desde el Carbonífero Superior (Béthoux, 2009). Los coleópteros, pese a ser un grupo abundante en El Soplao, no han sido estudiados por parte del doctorando debido a que el Sr. David Cerdán, miembro del equipo de investigación, lleva a cabo actualmente su Tesis Doctoral sobre los coleópteros del ámbar de España, los de El Soplao incluidos. No obstante, el estudio preliminar del abundante material de El Soplao ha identificado ejemplares pertenecientes a dos superfamilias y seis familias de escarabajos.

A.9.1. Subo. Adephaga: F. Carabidae Latreille, 1802

Existen más de 40000 especies descritas de esta gran familia cosmopolita de escarabajos omnívoros, aunque eminentemente depredadores y con casos documentados de fitofagia; típicamente sus miembros son habitantes de suelo, pero hay representantes que viven bajo la corteza de los árboles o entre la vegetación (Beutel & Leschen, 2005). Se han hallado dos ejemplares que podrían pertenecer a esta familia. Aunque el grupo no ha sido formalmente descrito en ámbar cretácico, sí ha sido reconocido en los ámbares del Líbano, Myanmar y Francia (Archingeay-Les Nouillers) (Kirejtshuk & Azar, 2008; Perrichot et al., 2010; Ross et al., 2010).

A.9.2. Subo. Polyphaga

A.9.2.1. Infrao. Staphyliniformia: Superf. Staphylinoidea: F. Staphylinidae Latreille, 1802

La familia Staphylinidae es la más abundantemente detectada en El Soplao, con cuatro ejemplares (Fig. 25A). Esta vastísima familia cosmopolita de coleópteros, con más de 50000 especies actuales descritas, es abundante en los ámbares del Líbano, Myanmar, Francia (Archingeay-Les Nouillers) y EUA (Nueva Jersey), habiéndose descrito algo más de una decena de especies entre todos ellos (véase Thayer et al., 2012). Acorde a su gran diversidad, los estafilínidos ocupan muchos tipos de hábitats y se alimentan de una gran variedad de recursos, siendo principalmente, tanto a nivel larvario como adulto, insectos depredadores, micófagos o saprofágicos (Thayer, 2005).

A.9.2.2. Infrao. Bostrichiformia: Superf. Bostrichoidea: F. Dermestidae Latreille, 1804

Existen algo más de 1000 especies de esta familia cosmopolita en la que las larvas se alimentan de materia animal o vegetal seca o recalcitrante, como queratina o quitina (Háva, 2004; Grimaldi & Engel, 2005). Se han identificado dos posibles derméstidos en El Soplao. En otros ámbares cretácicos, se han descrito ejemplares pertenecientes a esta familia en el Líbano y Myanmar (Cockerell, 1917; Kirejtshuk et al., 2009).

A.9.2.3. Infrao. Cucujiformia

A.9.2.3.1. Superf. Cucujoidea: F. Latridiidae Erichson, 1842

Se trata de una familia cosmopolita aunque relativamente pequeña, con alrededor de 1000 especies descritas, en las que tanto las larvas como los adultos se alimentan básicamente de materia vegetal en descomposición (Lord et al., 2010). En El Soplao existen tres ejemplares asignables a esta familia (Fig. 25B). El grupo ha sido descrito del ámbar del Líbano y ha aparecido también en los ámbares de Myanmar y la Federación de Rusia (Taimyr) (véase Kirejtshuk et al., 2009).

▲ **Fig. 25.** Escarabajos (Coleoptera) del ámbar de El Soplao. **A**. Estafilínido (Staphyliniformia: Staphylinoidea: Staphylinidae), CES 433.1. **B.** Ejemplar perteneciente a la familia Latridiidae (Cucujiformia: Cucujoidea). Escala = 0,5 mm (ambas subfiguras a la misma escala). Fotografías por David Cerdán.

A.9.2.3.2. Superf. Tenebrionoidea: F. Scraptiidae Mulsant, 1856

Los coleópteros de esta pequeña familia, en los casos mejor conocidos, se alimentan de polen en estado adulto, siendo polinizadores, mientras que las larvas se alimentan de madera muerta (Perkovsky & Odnosum, 2009). Un ejemplar de El Soplao ha sido asignado a

esta familia. Aunque se conoce que el grupo está presente en los ámbares de Myanmar, Francia (Archingeay-Les Nouillers) y Federación de Rusia (Taimyr) (Grimaldi et al., 2002; Perrichot et al., 2007), a día de hoy no se han publicado descripciones formales (véase Wang & Zhang, 2011)

A.9.2.3.3. Superf. Cleroidea: F. Cleridae Latreille, 1802

Se trata de una familia cosmopolita, con unas 3500 especies descritas, de escarabajos normalmente depredadores (típicamente de insectos xilófagos), aunque algunos se alimentan de polen o néctar u otros son carroñeros o saprófagos (Opitz, 2002). Se han hallado dos ejemplares asignables a la familia en el ámbar de El Soplao. Uno de ellos fue figurado por Najarro et al. (2010: fig. 8.5, anexo I.2). El grupo ha aparecido también en el ámbar de Myanmar (Ross et al., 2010).

A.9.2.4. Otros Polyphaga

Cuatro ejemplares pertenecientes a la superfamilia Elateroidea y dos asignados a la superfamilia Curculionoidea completan la diversidad detectada de escarabajos del suborden Polyphaga. Aunque ambas superfamilias se han hallado es los principales ámbares cretácicos, tan sólo algunos curculionoideos, de alimentación generalmente fitófaga (con formas barrenadoras de madera), han sido descritos del ámbar del Líbano, Myanmar, Francia (Archingeay-Les Nouillers) y EUA (Nueva Jersey) (Gratshev & Zherikhin, 2003; Perrichot et al., 2007; Cognato & Grimaldi, 2009; Kirejtshuk et al., 2009; Soriano, 2009).

A.10. O. HYMENOPTERA: Subo. Apocrita

El orden de los himenópteros, con más de 125000 especies actuales conocidas, cuenta con registro fósil desde el Triásico (Grimaldi & Engel, 2005). El orden se divide en dos subórdenes, los sínfitos y los apócritos, los primeros representando una agrupación parafilética. Aunque en El Soplao sólo existe registro de apócritos ello no es de extrañar, ya que en todo el ámbar de España tan sólo se conoce un sínfito, *Eosyntexis parva* Ortega-Blanco, Rasnitsyn & Delclòs, 2008, del ámbar de Peñacerrada I (Ortega-Blanco et al., 2008). El suborden Apocrita se subdivide clásicamente en los infraórdenes “Parasitica”, que es parafilético, y Aculeata.

A.10.1. Infrao “Parasitica”

A.10.1.1. Superf. Megalyroidea: F. Megalyridae Schletterer, 1889 - Pérez-de la Fuente et al. (2012b): anexo I.7

Los megalíridos representan hoy en día una pequeña familia de unas 50 especies clasificadas en ocho géneros distribuidos eminentemente en áreas tropicales del Hemisferio Sur, aunque también habitan el Sureste Asiático y Japón. Presentan un registro fósil de más de una decena de especies clasificadas en seis géneros extintos y uno vivo descritas de depósitos de ámbar que van desde el Cretácico Inferior hasta el Eoceno (véase Vilhelmsen et al., 2010). Ello indica que en el pasado la familia mostró una distribución y, posiblemente, una diversidad

mucho más amplias. Aunque la biología de los megalíridos sigue siendo muy desconocida, las observaciones indican que serían generalmente parasitoides idiobiontes (ésto es, el parasitoide mata al hospedador en el momento de la puesta) de cucarachas inmaduras y en menor medida de larvas de avispas esfécidas (Naumann, 1987; Shaw, 1990), ambos grupos encontrados en el ámbar de España (Peñalver & Delclòs, 2010). Se ha estudiado un ejemplar de El Soplao perteneciente a esta familia (CES 391.2), identificándose como el macho de *Megalava truncata* Perrichot, 2009. Esta especie se describió a partir de un ejemplar incompleto en ámbar de Peñacerrada I (Perrichot, 2009), con lo que el nuevo material ha permitido revisar la diagnosis del género †*Megalava* Perrichot, 2009 y ampliar el conocimiento de la especie. Representa una de las cuatro especies de insectos aparecidas tanto en El Soplao como en Peñacerrada I.

A.10.1.2. Superf. Evanioidea: F. Evaniidae Latreille, 1802 - Pérez-de la Fuente et al. (2012c): anexo I.8

En la actualidad, los evánidos son avispas cosmopolitas, aunque están presentes mayoritariamente en los trópicos, y principalmente tienen hábitos depredadores solitarios de huevos de cucaracha dentro de sus ootecas (Deans & Whitfield, 2003; Deans, 2005). Su registro fósil es muy abundante, conociéndose alrededor de una decena de géneros mesozoicos, el más diverso de los cuales, con más de una decena de especies conocidas, es el género †*Cretevania* Rasnitsyn, 1975 (Peñalver et al., 2010). La nueva especie de El Soplao, *Cretevania soplaensis* Pérez-de la Fuente, Peñalver & Ortega-Blanco, 2012 (CES 364.2), incrementa aún más la elevada diversidad de este género en el ámbar de España, descrita en los ámbares de Peñacerrada I, San Just y Arroyo de la Pascueta (ibid.). La elevada diversidad de evánidos pudo estar relacionada con una especial abundancia de cucarachas en el territorio ibérico durante el Cretácico Inferior (ibid.). Por otra parte, tres evánidos más han sido identificados recientemente (CES 450.1, 578 y 603.1), mientras que se ha identificado un evanioideo (CES 383) (Fig. 26) perteneciente a la familia Aulacidae Shuckard, 1841 o Gasteruptiidae Ashmead, 1900.

A.10.1.3. Clado Proctotrupomorpha

Este linaje de apócritos, la monofilia del cual está bien establecida, reúne a la mayoría de pequeños parasitoides existentes en el orden Hymenoptera (o “microhimenópteros”), representado un grupo extremadamente diverso (Grimaldi & Engel, 2005). De esta agrupación se conocen en El Soplao las superfamílias Serphitoidea (Serphitidae y Mymarommatidae) y Platygastroidea (Platygastridae).

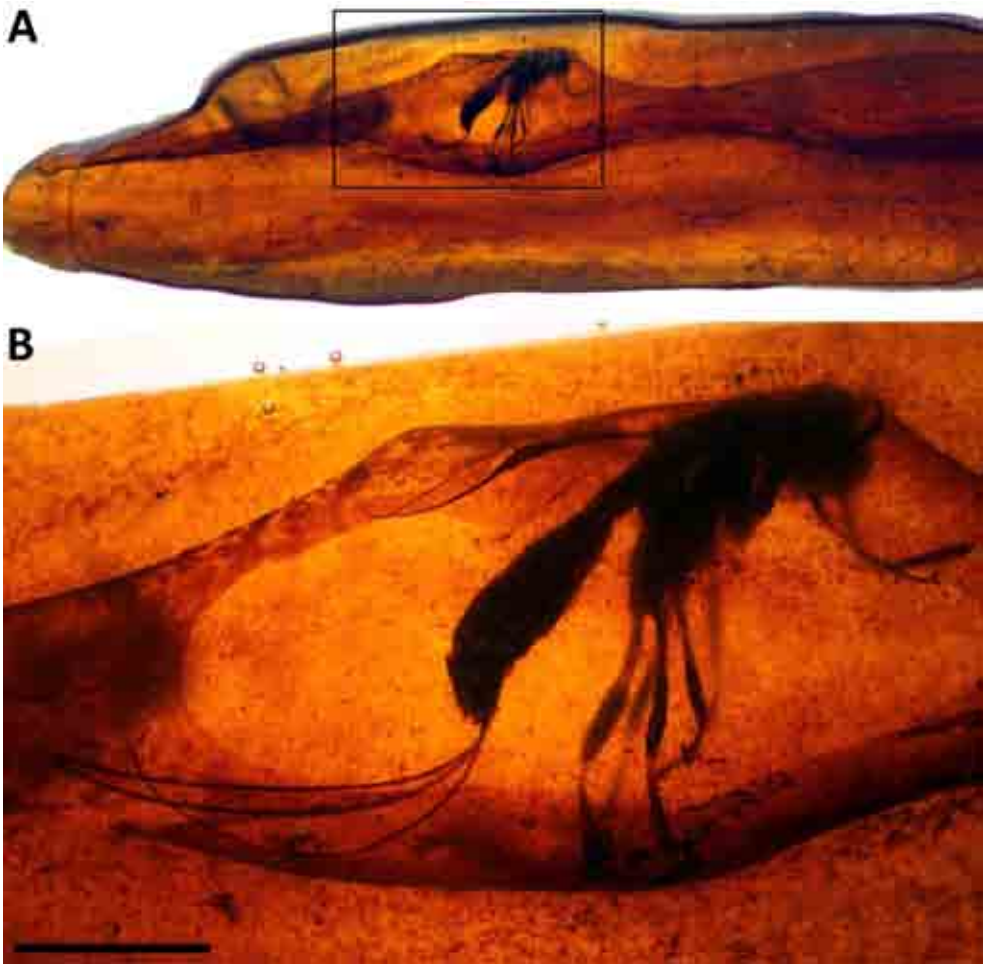
A.10.1.3.1. Superf. Serphitoidea

Se clasifican en esta superfamilia avispas proctotrupomorfas de biología incierta, aunque se asume que sean parasitoides. Ortega-Blanco et al. (2011a) han sugerido la sinonimia de esta superfamilia con Mymarommatoidea, en parte tras el estudio de ejemplares de El Soplao. Un ejemplar (CES 355) podría pertenecer a la familia †Alavarommatidae Ortega-Blanco, Peñalver, Delclòs & Engel, 2011, representada únicamente por la especie *Alavaromma*

orchamum Ortega-Blanco, Peñalver, Delclòs & Engel, 2011 del ámbar de Peñacerrada I. Esta especie se emparenta con las avispas serfítidas, hoy extintas.

A.10.1.3.1.1. F. †Serphitidae Brues, 1937

De esta esta familia únicamente se conocen 16 especies repartidas en cuatro géneros procedentes de los ámbares de España, Myanmar, EUA (Nueva Jersey), Federación de Rusia (Taimyr) y Canadá (Engel et al., 2011). Así pues, las especies descritas del ámbar de España, corresponden a los registros más antiguos. En relación a El Soplao, Ortega-Blanco et al. (2011a) describieron *Microserphites soplaensis* Ortega-Blanco, Delclòs, Peñalver & Engel, 2011 (CES 566.1) (Fig. 27A). Este ejemplar reviste especial importancia filogenética al presentar caracteres compartidos entre las superfamilias Serphitoidea y Mymarommatoidea. Otros tres serfítidos más han sido hallados en El Soplao (CES 315.3, 402.8 y 417).



▲ **Fig. 26.** Evanioideo del ámbar de El Soplao perteneciente a la familia Aulacidae o Gasteruptiidae (Hymenoptera: Apocrita: Evanioidea), CES 383. **A**. Vista general de la pieza que contiene la inclusión, resultado de dos flujos sucesivos de resina. **B**. Área enmarcada en A. Escala = 1 mm.

A.10.1.3.1.2. F. Mymarommatidae Debauche, 1948

La familia Mymarommatidae representa el único linaje vivo de la superfamilia Serphitoidea y también el más diverso, pese a contar con poco más de una decena de especies actuales descritas en todos los continentes, y algo más de una decena de especies fósiles procedentes de los ámbares cretácicos de España, Myanmar, Federación de Rusia (Taimyr: Nizhnyaya Agapa), EUA (Nueva Jersey), Japón y Canadá, así como algunos ámbares cenozoicos. Ortega-Blanco et al. (2011b) describieron esta familia a partir del ejemplar alotipo de *Archaeromma hispanicum* Ortega-Blanco, Peñalver, Delclòs & Engel, 2011 de El Soplao (CES 452) (Fig. 27B) y del holotipo hallado en el ámbar de Peñacerrada I. Ésta es una de las cuatro especies que han sido halladas en El Soplao y Peñacerrada I. El género †*Archaeromma* Yoshimoto, 1975 representa el grado más ancestral conocido en la familia. Existen en El Soplao cuatro ejemplares adicionales identificados como Mymarommatidae (CES 391.5, 402.2, 454 y 504).

▲ **Fig. 27.** Avispas proctotrupomorfas del ámbar de El Soplao (Hymenoptera: Apocrita). **A**. Holotipo de *Microserphites soplaensis* Ortega-Blanco, Delclòs, Peñalver & Engel, 2011 (†Serphitidae), CES 566.1. **B**. Alotipo de *Archaeromma hispanicum* Ortega-Blanco, Peñalver, Delclòs & Engel, 2011 (Mymarommatidae), CES 452. **C–D**. Ejemplares de platigástridos "esceliónidos" (Platygastroidea: Platygastridae), CES 130.1 y CES 470, respectivamente. Escalas: A, B = 0,2 mm; C, D = 0,5 mm. Fotografías (excepto C) por Enrique Peñalver.

A.10.1.3.2. Superf. Platygastroidea: F. Platygastridae Haliday, 1833

Este grupo de diminutas avispas proctotrupomorfas endoparasitoides idiobiontes de huevos de artrópodos, de unas 4500 especies actuales de distribución mundial (Austin et al., 2005), presenta una elevada abundancia en el ámbar de El Soplao, con alrededor de 90 ejemplares. El grupo se conoce con el término de esceliónidos, aunque las clasificaciones actuales tiendan a considerarlo subfamilia de Platygastridae (Sharkey, 2007; Murphy et al.,

2007). Pese a ello, el estudio de la diversidad cretácica del grupo aún no se ha acometido por su complejidad, debido a su elevada abundancia, su pequeño tamaño y su simplicidad morfológica, que limita los caracteres de importancia diagnóstica. No obstante, los doctores Jaime Ortega-Blanco, Ryan McKellar y Michael Engel están finalizando una monografía que estudia este grupo en el ámbar de Peñacerrada I, y que corresponde al primer esfuerzo para categorizar la elevada diversidad de este grupo en ámbar cretácico. Dicha monografía constituirá una importante base documental para abordar el estudio de los ejemplares de El Soplao (Fig. 27C, D; Najarro et al., 2009: fig.12B, anexo I.1). Aun así, Ortega-Blanco (2010) detectó una especie común en los ámbares de Peñacerrada y El Soplao, mientras que una revisión preliminar de parte del material de platigástridos de El Soplao ha permitido reconocer posteriormente un nuevo morfotipo (CES 011).

A.10.1.3.3. Otros proctotrupomorfos

Se han hallado dos ejemplares (CES 398 y 402.3) pertenecientes a la familia †Stigmaphronidae Kozlov, 1975, constituida por ceraphronoideos exclusivamente cretácicos de biología desconocida (Engel & Grimaldi, 2009; Ortega-Blanco et al., 2011c), y un posible registro de la familia Mymaridae Haliday, 1833 (CES 450.2), que son chalcidoideos actualmente parasitoides de insectos (Huber, 1986).

A.10.1.4. Otros apócritos "Parasitica"

Cinco ejemplares clasificados en la enigmática familia cretácica †Maimetshidae Rasnitsyn, 1975 (CES 018.1 + 018.2 + 018.3, 386 y 397), de biología incierta (Perrichot et al., 2011), y un ichneumonoideo Braconidae Nees von Esenbeck, 1811 (CES 430), parasitoides idio- o cenobiontes de insectos (Wharton, 1993), pertenecen a este grupo. Los bracónidos son en la actualidad muy diversos, con más de 20000 especies de distribución mundial (Huber, 2009).

A.10.2. Infrao. Aculeata

Finalmente, destacar la presencia de varios grupos de himenópteros aculeados, de distribución mundial y típicamente parasitoides de larvas de insecto, poco frecuentes en ámbar debido a su, por lo general, gran tamaño en términos relativos (Ortega-Blanco, 2010; McKellar & Engel, 2012). Dentro de la superfamilia Chrysidoidea, se ha identificado un ejemplar asignable a la familia Bethylidae Forster, 1856 (CES 384), constituida en la actualidad por especies parasitoides de larvas de lepidópteros y coleópteros, y otro ejemplar considerado dentro de la familia Chrysididae Latreille, 1802 (CES 530.4), parasitoides o cleptoparásitos de lepidópteros, fásmidos o himenópteros (Kimsey & Bohart, 1990). Asimismo, se han identificado tres posibles Tiphiidae (CES 130.5 + 130.6 y 316.6), vespoideos nectarívoros típicamente parasitoides de larvas de coleóptero (Engel et al., 2009b).

A.11. O. MECOPTERA

La diversidad actual de estos insectos, de unas 600 especies, es un relicto de la diversidad pasada, que se remonta hasta el Pérmico y es de unas 400 especies fósiles conocidas clasificadas en una veintena de familias (Grimaldi & Engel, 2005). Pese a ello, los

mecópteros son muy escasos en ámbar cretácico, puesto que tan sólo existen dos especies del ámbar de Myanmar clasificadas en el género †*Parapolycentropus* Grimaldi & Rasnitsyn, 2005, pertenecientes a la familia †Pseudopolycentropodidae Handlirsch, 1925 (Grimaldi et al., 2005). Estos mecópteros se caracterizan por la presencia de un aparato bucal grácil de tipo chupador. El ejemplar de El Soplao (CES 437, Fig. 28) corresponde a un morfotipo diferente del descrito de Myanmar, al presentar diferencias por ejemplo en las antenas y terminalia.

▲ **Fig. 28.** Mecóptero indeterminado del ámbar de El Soplao (Mecoptera). **A**. Hábito lateral. **B**. Hábito ventral. Escala = 1 mm (ambas subfiguras a la misma escala).

A.12. O. DIPTERA

Este gran orden de insectos cuenta con más de 150000 especies actuales descritas (Evenhuis et al., 2008). Aunque Diptera se hubiera escindido de su ancestro mecopteroide alrededor del límite Permo-Triásico, no se conocen fósiles de dípteros anteriores al Triásico Inferior/Medio (Krzemiński & Krzemińska, 2003). De los dos subórdenes en los que el orden se divide, los nematóceros representan una agrupación parafilética (véase Bertone et al., 2008).

A.12.1. Subo. "Nematocera"

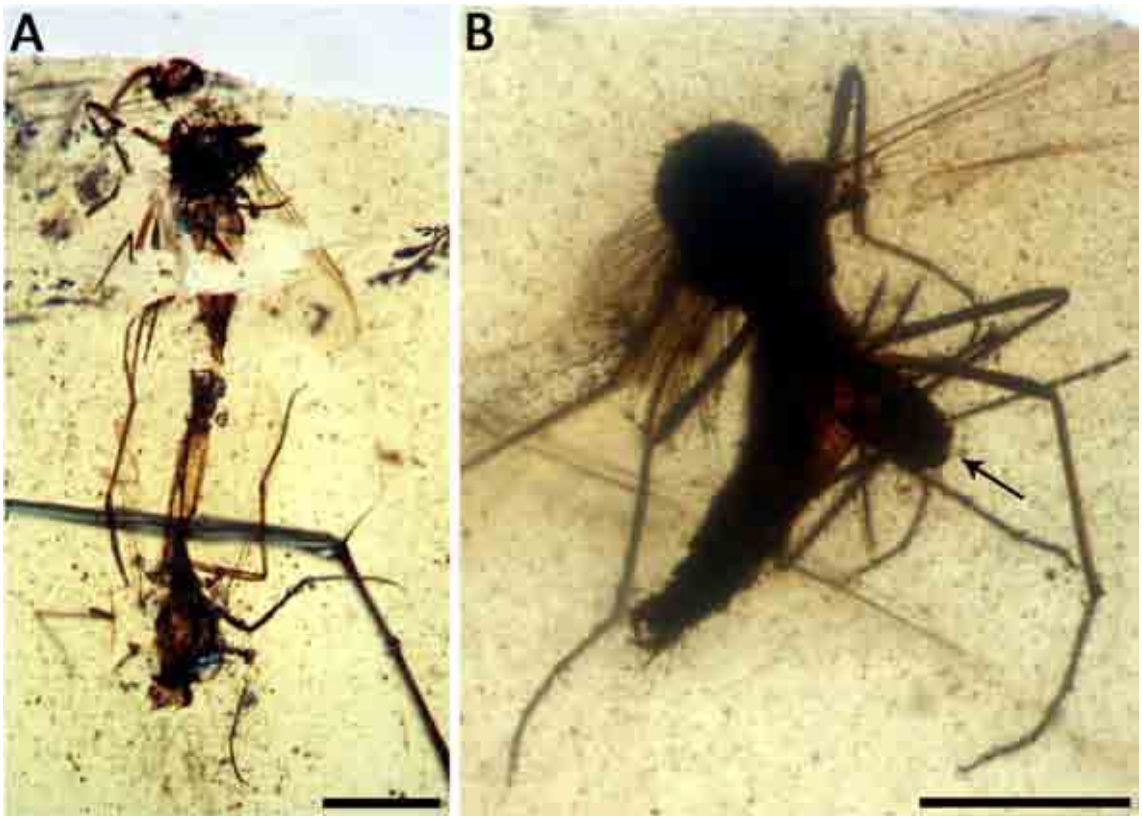
A.12.1.1. Infrao. Culicomorpha

A.12.1.1.1. F. Ceratopogonidae Newman, 1834 - Pérez-de la Fuente et al. (2011): anexo I.5

Los mosquitos ceratopogónidos son dípteros nematóceros muy pequeños, que poseen una gran variedad de hábitos alimenticios (hematofagia, depredación, polinivorismo, nectarivorismo y afagia) y estadios larvarios que generalmente se desarrollan en ambientes semiacuáticos o húmedos (Borkent, 1995). Mientras que actualmente se conocen unas 6000 especies distribuidas mundialmente, su diversidad en los yacimientos de ámbar desde el Cretácico Inferior es elevada, con unas 250 especies fósiles descritas (Borkent, 2012).

Cinco géneros (uno de ellos actual) han sido hallados en El Soplao: †*Lebanoculicoides* Szadziewski, 1996, †*Archiaustroconops* Szadziewski, 1996, †*Protoculicoides* Boesel, 1937, †*Atriculicoides* Remm, 1976 y *Austroconops* Wirth & Lee, 1958. Todos estos géneros pertenecen al linaje más ancestral de la familia, presente en Laurasia ya durante el Cretácico Inferior. Además, tanto los estudios filogenéticos (Borkent, 1995; Szadziewski, 1996) como los de morfología comparada (Szadziewski & Schlüter, 1992; Borkent, 1995, 2000a,b) indican que estos ceratopogónidos ancestrales fueron hematófagos, muy posiblemente alimentándose de la sangre de los dinosaurios. El género †*Lebanoculicoides* se considera el linaje más ancestral de la familia por la retención de una plesiomorfía alar (Szadziewski, 1996; Borkent, 2000). Este género queda representado en El Soplao por *Lebanoculicoides excantabris* Pérez-de la Fuente, Delclòs, Peñalver & Arillo, 2011 (ES-07-09). Antes de la descripción de esta especie, el género era tan sólo conocido por una especie en ámbar del Líbano, *L. mesozoicus* Szadziewski, 1996. La presencia de *L. excantabris* en la Península Ibérica durante el Cretácico Inferior amplía notablemente el rango paleobiogeográfico del género, y sugiere una historia evolutiva que podría remontarse al Jurásico. Otros ejemplares asignables a este género son CES 411, 420.5, 316.10 y 423.1 + 423.2. Estas dos últimas sininclusiones corresponden a dos individuos en cópula, hecho extraordinario en Paleontología (Fig. 29A) y que permite establecer de forma inequívoca las características del macho y de la hembra para una especie fósil. En este caso se ha observado que existía un marcado dimorfismo sexual. El género †*Protoculicoides* se basa en cinco especies descritas de los ámbares del Líbano, España, Myanmar y Canadá. La especie hallada en El Soplao corresponde a una de ellas, *Protoculicoides skalskii* Szadziewski & Arillo, 1998 (ES-07-18), que fue antes descrita en Peñacerrada I y hallada posteriormente en San Just (Szadziewski & Arillo, 1998; Arillo et al., 2008b). Por tanto, tras su descripción en El Soplao, esta especie es común a los tres principales yacimientos españoles de ámbar cretácico. Se han hallado dos ejemplares más asignados a este género (CES 416 y 603.7). El género

†*Archiaustroconops* se había hallado anteriormente en los ámbares del Líbano, España (Peñacerrada I) y Myanmar. Está representado en El Soplao por la especie *Archiaustroconops borkenti* Pérez-de la Fuente, Delclòs, Peñalver & Arillo, 2011 (ES-07-17) y varios ejemplares no determinados a nivel de especie (CES 420.3, 442, 513, 558.1 + 558.2 y 587.2). El género †*Atriculicoides* está compuesto por un total de ocho especies procedentes de los ámbares de Myanmar, Francia, Federación de Rusia (Taimyr) y Canadá. La nueva especie de El Soplao, *Atriculicoides szadziewskii* Pérez-de la Fuente, Delclòs, Peñalver & Arillo, 2011 (CES 363), se añade a esa lista y representa la especie más antigua descrita de este género. Además, ha sido identificado otro ejemplar asignable al género (CES 402.5). Finalmente, el género *Austroconops* ha sido reconocido en El Soplao (CES 008 y 017.1). Se han hallado otros ejemplares posiblemente pertenecientes a este género (CES 368 y 413.2). El género está actualmente restringido a dos especies del oeste de Australia, mientras que se conocen siete especies fósiles descritas de los ámbares del Líbano, Myanmar, Bezonnais (Francia) y Federación de Rusia (Taimyr). Las larvas tanto de este género como del género *Leptonocops* Skuse, 1889, el otro fósil viviente de la familia, de distribución pantropical, viven actualmente enterrados en suelos húmedos, como arenas de playas o fangos de marjales costeros (Downes & Wirth, 1981; Borkent, 2001; Borkent & Craig, 2004). Ambos géneros relictos han sido siempre hallados conjuntamente, a menudo como sininclusiones, en los principales ámbares del Cretácico Inferior, ésto es, del Líbano, España y Myanmar. La presencia del género *Austroconops* en El Soplao sugiere que la línea de costa se encontraba cerca de las plantas resiníferas.



▲ **Fig. 29.** Inclusiones de dípteros nematóceros culicomorfos (Diptera: Culicomorpha) del ámbar de El Soplao con importancia paleoetológica. **A**. Macho y hembra pertenecientes al género †*Lebanoculicoides* (Ceratopogonidae) en posición de cópula. **B**. Mosquito quironómido (Chironomidae) ectoparasitado por un ácaro indeterminado (flecha). Escalas = 0,5 mm.

A.12.1.1.2. F. Chironomidae Macquart, 1838

La familia Chironomidae es un grupo cosmopolita y muy diverso, con unas 5000 especies actuales y un abundante registro fósil desde el Triásico (Grimaldi & Engel, 2005). Sus larvas viven en ambientes acuáticos o semiacuáticos, mientras que los adultos son áfagos o si se alimentan lo hacen normalmente de exudados vegetales, si bien existen algunos pocos casos de hematofagia (Azar & Nel, 2012). Se conocen varios ejemplares de El Soplao (CES 315.6, 358, 377.1, 531.1, 562.2, 596 y 604). El ejemplar 531.1 quedó englobado por la resina mientras era ectoparasitado por un ácaro indeterminado (Fig. 29B).

A.12.1.2. Infrao. Psychodomorpha: F. Psychodidae Newman, 1834

Los psicódidos son un grupo cosmopolita y diverso, con más de 3000 especies y un registro abundante en ámbar (Grimaldi & Engel, 2005). Varios ejemplares pertenecientes a esta familia han sido identificados (CES 401.6 y 527.2), dos de ellos reconocidos dentro de la subfamilia Phlebotominae Rondani, 1840 como el género †*Eophlebotomus* Cockerell, 1920 (CES 359 y 530.20), basado en tres especies de los ámbares del Líbano, Myanmar y Francia (Azar et al., 2003). Mientras que las larvas actuales de los flebotóminos son detritívoras, las hembras adultas son hematófagas y pueden ser transmisoras de enfermedades como la leishmaniasis (Lehane, 2005).

A.12.1.3. Infrao. Bibionomorpha: F. Cecidomyiidae Newman, 1835

Únicamente se ha hallado un ejemplar perteneciente a la familia Cecidomyiidae (CES 562.3), muy diversa actualmente (unas 5000 especies), quizá clasificable en el género †*Eltxo* Arillo & Nel, 2000, descrito del ámbar de Peñacerrada I por Arillo & Nel (2000). Estos autores también describieron el género †*Cretohaplusia* Arillo & Nel, 2000. Otras especies cretácicas han sido descritas del ámbar de Canadá (Gagné, 2010). Aunque su condición primitiva implica una alimentación fungívora, actualmente las larvas de cecidómidos se alimentan típicamente de tejidos de plantas, tras haber inducido una agalla en la planta huésped en la que primero la larva pupa y luego el adulto emerge. Los adultos son áfagos o se alimentan de exudados normalmente vegetales (Gagné, 1994). Otro cecidómido fue figurado por Najarro et al. (2009: fig. 12C, anexo I.1), pero no ha sido aún registrado en la colección por hallarse en proceso de preparación.

A.12.2. Subo. Brachycera

A.12.2.1. Infrao. Stratiomyomorpha: F. †Zhangsolvidae Nagatomi & Yang, 1998

Los estratiomorfos representan el linaje de braquíceros más ancestral que existe (Grimaldi & Engel, 2005). Dentro de éstos, la familia †Zhangsolvidae es el grupo más basal conocido, caracterizado por una larga probóscide ensanchada apicalmente. Dicho grupo era tan sólo previamente conocido por tres géneros y especies procedentes de yacimientos jurásico-cretácicos de compresión de China y Brasil, ésto es, *Zhangsolva cupressa* (Zhang, Zhang & Li, 1993), *Cratomyia macrorrhyncha* Mazzarolo & Amorim, 2000 y *Cratomyoides cretacicus* Wilkommen, 2007 (Zhang et al., 1993; Mazzarolo & Amorim, 2000; Wilkommen & Grimaldi, 2007). Los tres taxones presentan una deficiente preservación. Por tanto, los nuevos

ejemplares preservados en ámbar de El Soplao, dos hembras y un macho que se describirán como un nuevo género y especie, suponen un avance muy sustancial en el conocimiento tanto morfológico y filogenético como autopaleoecológico de este primitivo grupo de dípteros, y por tanto de la evolución del suborden Brachycera. Los tres ejemplares se hallaron originalmente en la misma pieza de ámbar y por tanto son sininclusiones. Una de estas hembras (Fig. 30A) y el macho se han preparado en dos piezas de ámbar, preservando cada una de ellas partes de ambos (la hembra correspondiendo a las siglas CES 015.2 y 392.2, y el macho a CES 015.3 y 392.3), mientras que la otra hembra (CES 349.1, Fig. 30B) se halla en una preparación aparte. La descripción original de un taxón fósil basado en ambos sexos únicamente se produce en casos muy excepcionales, como en este en el que se han hallado como sininclusiones. Gracias a la buena preservación de los ejemplares, ha sido posible aislar un fino corte en sección de la probóscide de una de las hembras (Fig. 30C), y se ha podido concluir que estos dípteros eran nectívoros, algo que ya había sido sugerido previamente (Grimaldi et al., 2011). Muy posiblemente, se alimentaron de néctar de plantas del grupo de las Bennettitales, como ha sido sugerido para algunos mecópteros fósiles del Jurásico y el Cretácico con probóscides análogas que, además, posiblemente actuaron como polinizadores (Ren et al., 2009). Asimismo, estos singulares dípteros de El Soplao presentan un curioso dimorfismo sexual, ya que las antenas del macho son del orden de cuatro veces más largas que las de la hembra.

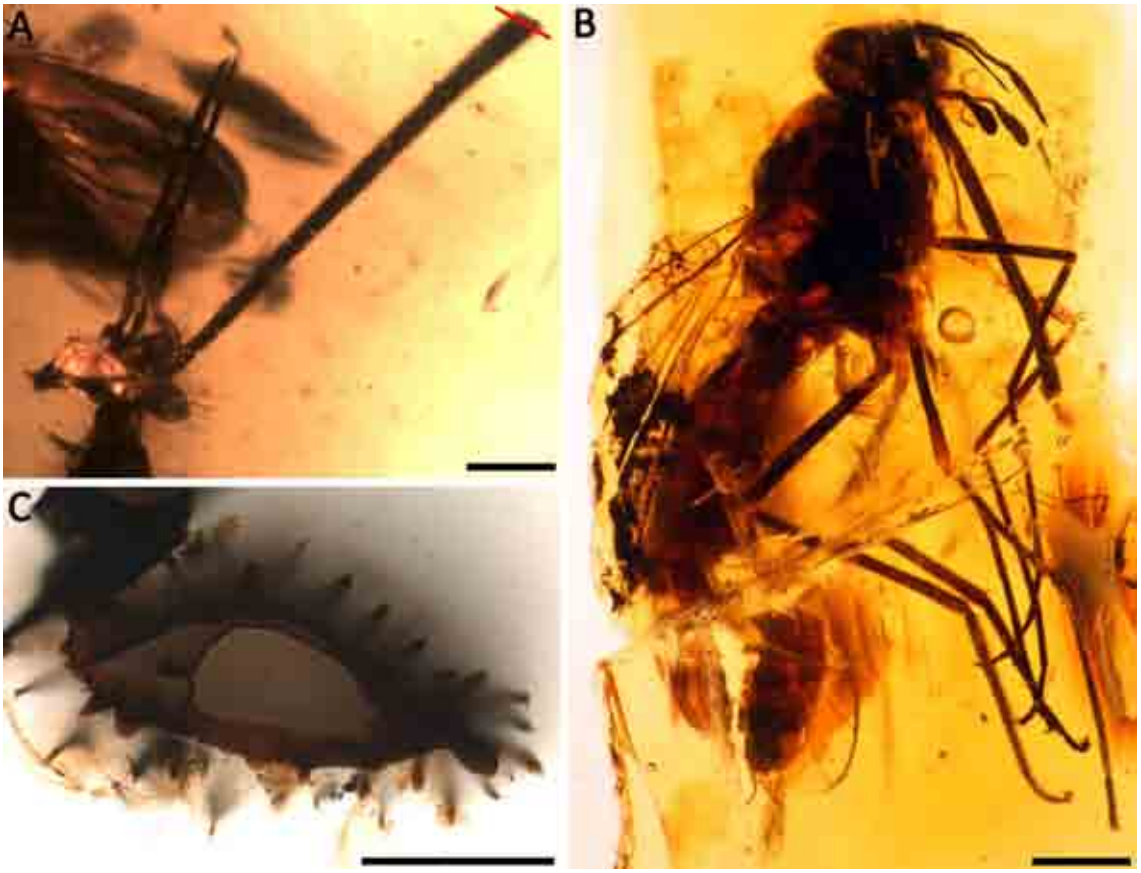
A.12.2.2. Infrao. Tabanomorpha: F. Rhagionidae Latreille, 1802

Esta familia cosmopolita de unas 700 especies distribuidas en unos 50 géneros (Santos, 2008) posee registro desde el Triásico, aunque adquiere una diversidad muy notable en el Jurásico Medio (véase Solórzano-Kraemer & Nel, 2009). En El Soplao se ha reconocido un ejemplar asignable al género *Litoleptis* Chillcott, 1963 (CES 360). Este género ha sido descrito en el ámbar de San Just como *L. fossilis* Arillo, Peñalver & García-Gimeno 2009, y es conocido en la fauna actual de China, Nepal, Filipinas, Japón, Alaska y Chile (véase Arillo et al., 2009). El género pertenece a la subfamilia Spaniinae, que, aunque ha llegado a considerarse una familia a parte, las clasificaciones recientes tienden a mantenerlo en la familia Rhagionidae (Kerr, 2010). Aunque la condición general de los ragiónidos adultos es la depredadora, dentro de esta subfamilia se dan casos de hematofagia (Lehane, 2005). Otros registros indeterminados de esta familia corresponden a las siglas CES 588 y CES 530.1.

A.12.2.3. Clado Eremoneura

A.12.2.3.1. Superf. Empidoidea

Este grupo de eremoneuros basales, con más de 11000 especies repartidas a nivel mundial y hábitos depredadores tanto a nivel larvario como adulto, corresponde a los braquíceros más comúnmente hallados en los ámbares cretácicos (Grimaldi & Cumming, 1999; Grimaldi & Engel, 2005; Sinclair & Cumming, 2006). Las larvas suelen estar asociadas a sustratos húmedos (Brown et al., 2010).



▲ **Fig. 30.** Ejemplares asignados a un nuevo género y especie perteneciente a la familia †Zhangsolvidae (DIptera: Brachycera: Stratiomyomorpha) del ámbar de El Soplao. **A**. Detalle de la cabeza y probóscide incompleta de la hembra con sigla CES 015.2. **B**. Hábito lateral de la hembra con sigla CES 349.1. **C**. Sección de la probóscide de CES 015.2, aislado a partir de la probóscide incompleta del ejemplar (línea roja en A). Escalas: A = 1 mm; B = 0,5 mm; C = 0,05 mm. Fotografía C por Enrique Peñalver.

A.12.2.3.1.1. F. Atelestidae Hennig, 1970

Se han hallado dos ejemplares pertenecientes al conocido como "grupo del género *Nemedina* Chandler, 1981", CES 379.1, 523 y 528. CES 523 es quizá asignable al género †*Nemedromia* Grimaldi & Cumming, 1999, mientras que CES 528 pertenece al género *Nemedina*. Durante dos décadas la filogenia de este grupo ha sido enigmática, en parte debido a que tan sólo se conocía un espécimen vivo descrito de Hungría (Chandler, 1981). Posteriormente, se describieron ocho especies fósiles clasificadas en cuatro nuevos géneros, entre ellos †*Nemedromia*, a partir del registro en los ámbares del Líbano, EUA (Nueva Jersey) y Canadá (Grimaldi & Cumming, 1999). Asimismo, más tarde se describieron nuevos registros del género *Nemedina* correspondientes a una nueva especie en ámbar del Báltico y dos registros adicionales en la fauna actual (Sinclair & Papp, 2004). El grupo del género *Nemedina* fue finalmente asignado a la familia Atelestidae por Sinclair & Cumming (2006), y se considera que es el grupo hermano del resto de empidoideos. La diversidad conocida del grupo sugiere que se trata de un linaje relicto.

A.12.2.3.1.2. F. Hybotidae Chvála, 1983

Se han identificado cuatro especímenes pertenecientes al género †*Trichinites* Hennig, 1970 (CES 372, 404.1 + 404.2 y 439) (Hennig, 1970). Este género se considera el grupo

hermano del resto de Hybotidae y es conocido únicamente hasta ahora por una especie del ámbar del Líbano, *T. cretaceus* Hennig, 1970 (Grimaldi & Cumming, 1999), de ahí que todo nuevo hallazgo revista de especial relevancia.

A.12.2.3.1.3. F. Dolichopodidae Latreille, 1809

Esta familia alberga alrededor de 7000 especies actuales de distribución mundial (Grimaldi & Engel, 2005). Si se compara con esta diversidad, unos pequeños grupos de empidoideos diversificados en el Cretácico fueron incorporados a Dolichopodidae por Sinclair & Cumming (2006) en dos subfamilias, Microphorinae y Parathalassiinae, representado linajes basales de Dolichopodidae. En El Soplao se han hallado tres especímenes pertenecientes al género †*Microphorites* Hennig, 1971 (CES 396.1 + 396.2 y 440; Fig. 31A), clasificados en la subfamilia Microphorinae. Conforman la diversidad descrita del género cuatro especies del ámbar del Líbano, una especie del ámbar de España (San Just) y una especie del ámbar de Francia (Archingeay-Les Nouillers), aunque el género está también bien presente en otros yacimientos de ámbar de España (Peñacerrada I) y Myanmar (Grimaldi & Cumming, 1999; Nel et al., 2004b; Grimaldi & Engel, 2005; Arillo et al., 2008b). Otros ejemplares quizá correspondientes a este género son CES 389.3 y 413.4. Por otra parte, se han identificado dos ejemplares asignados provisionalmente al género †*Cretomicrophorus* Negrobov, 1978 (CES 530.21 + 530.22), pertenecientes a la subfamilia Parathalassiinae. Este género ha sido descrito anteriormente en los ámbares de EUA (Nueva Jersey) y Federación de Rusia (Taimyr) (Grimaldi & Cumming, 1999). Dicha subfamilia representa el grupo hermano del resto de Dolichopodidae (Sinclair & Cumming, 2006).

Aunque los adultos actuales de algunas especies del género *Microphorella* Becker, 1909 se han hallado asociados a cursos de agua en tierra firme, la mayoría de los miembros clasificados en la subfamilia Parathalassiinae presentan en su estado adulto hábitos de vida ligados al litoral marino, asumiéndose que sus larvas viven en la zona intermareal (Ulrich, 2004). Por otra parte, de los dos géneros actuales clasificados en la subfamilia Microphorinae, *Microphor* Macquart, 1827 retiene los hábitos de vida en tierra firme, ya que sus larvas se desarrollan en los suelos de los bosques (hábito que se considera que es la condición ancestral de Empidoidea) (ibid.), pero las observaciones sobre las especies del género *Schistostoma* Becker, 1902 indican hábitos asociados a menudo a arenas litorales (Pârvu & Popescu-Mirceni, 2007). También se ha indicado que la genitalia femenina en el género †*Microphorites* pudiera ser una adaptación a la ovoposición en arenas de playas (Nel et al., 2004b). Por tanto, cabe esperar que la presencia de estos linajes basales de la familia Dolichopodidae en El Soplao tenga su origen en la proximidad de la paleolínea de costa a las plantas emisoras de resina. Esto mismo se deduce de la presencia en ámbar de los géneros de mosquitos ceratopogónidos *Leptoconops* y *Austroconops*, este último aparecido en El Soplao (apartado A.12.1.1.1). En este sentido, es destacable que los géneros †*Microphorites* y *Leptoconops* hayan aparecido como sininclusiones en el ámbar de San Just (Arillo et al., 2008b).

A.12.2.3.2. F. †Chimeromyiidae Grimaldi & Cumming, 2009

Este grupo conocido únicamente del Cretácico Inferior representa un grado intermedio entre Empidoidea y Cyclorrhapha, hecho que tentativamente lleva a considerarlo un linaje

mayor de eremoneuros (Grimaldi et al., 2009). Dos géneros componen la familia: el género †*Chimeromyia* Grimaldi & Cumming, 1999, basado en siete especies de los ámbares del Líbano, España (Peñacerrada I) y Myanmar, y el género †*Chimeromyina* Arillo & Grimaldi, 2009, basada en una única especie del ámbar español de Peñacerrada I (Grimaldi & Cumming, 1999; Grimaldi et al., 2009). En El Soplao, tres ejemplares son asignables al género †*Chimeromyia* (CES 352.1, 438 y 562.1). El primero de estos ejemplares representa una nueva especie (Fig. 31B). Otros ejemplares reconocidos dentro de esta familia son CES 364.8 y 570.2.

▲ **Fig. 31.** Eremoneuros (Diptera: Brachycera) del ámbar de El Soplao. **A**. Ejemplar perteneciente al género †*Microphorites* (Empidoidea: Dolichopodidae), CES 440. **B**. Ejemplar reconocido como una nueva especie del género †*Chimeromyia* (Chimeromyiidae), CES 352.1. Escalas: A = 1 mm; B = 0,5 mm. Fotografía A por Rafael López del Valle.

A.12.2.3.3. Clado Cyclorrhapha: F. Phoridae Curtis, 1833

Esta familia de ciclorrafos basales, de alrededor de 6000 especies actuales, presenta actualmente una diversidad de modos de vida extraordinaria, con formas saprófagas (como es la norma para los ciclorrafos), pero también fitógafas, depredadoras y parasitoides que pueden llegar a ser altamente especializadas (Disney, 1994). La diversidad descrita en los ámbares cretácicos corresponde a una primera radiación mesozoica independiente de la radiación cenozoica que dio lugar a la diversidad actual (Grimaldi & Engel, 2005). Esta diversidad cretácica se basa en un género descrito de los ámbares de Francia (Archingeay-Les Nouillers), EUA (Nueva Jersey), Canadá y Federación de Rusia (Taimyr), cuatro géneros del ámbar de este último país y un género del ámbar de español de Peñacerrada I (Solórzano-Kraemer et al., 2011). Este último corresponde al género †*Euliphora* Arillo & Mostovski, 1999, descrito a partir de una única especie, y representa el género más antiguo de esta diversidad basal de la familia (Arillo & Mostovski, 1999). En El Soplao se han reconocido siete ejemplares pertenecientes a este género (CES 532.1 + 532.2, 533.1 + 533.2, 535, 538 y 540), los cuales se hallaron en una misma pieza de ámbar, representando así un posible caso de enjambramiento. Un ejemplar adicional tiene por sigla CES 434.

A.13. O. LEPIDOPTERA

Con alrededor de 175000 especies descritas (Mallet, 2007), los lepidópteros representan uno de los cuatro grandes órdenes de insectos en términos de diversidad actual, junto a coleópteros, himenópteros y dípteros. De los cinco ejemplares de lepidópteros descubiertos en El Soplao, al menos uno (CES 392.1) se ha asignado a la familia Micropterigidae Herrich-Schäffer, 1855. Este primitivo grupo de polillas, que es grupo hermano del resto de lepidópteros y cuenta con alrededor de un centenar de especies actuales descritas, retiene mandíbulas funcionales y es detritívoro, no habiendo desarrollado la probóscide típica del grupo (Grimaldi & Engel, 2005). Existen descritas una especie del ámbar del Líbano y otra del ámbar de Myanmar (Grimaldi, 1999; Grimaldi & Engel, 2005). Actualmente, el Dr. Antonio Arillo y la Sra. Estefanía Mas estudian los lepidópteros del ámbar de El Soplao (Fig. 32) y de otros ámbares españoles.

▲ **Fig. 32.** Polilla (Lepidoptera) del ámbar de El Soplao, CES 407. Escala = 1 mm. Fotografía por Rafael López del Valle.

6.3.2. = B. SUBFILO CHELICERATA: CL. ARACHNIDA

B.1. O. ARANEAE

Se tiene registro de arañas desde el Carbonífero Superior (Penney & Selden, 2011), conociéndose actualmente una diversidad de alrededor de 43000 especies (Platnick, 2012). Además de los grupos expuestos a continuación, dos arañas más (CES 016.1 y 476.1) se han asignado provisionalmente a la familia Araneidae Clerck, 1758.

B.1.1. Superf. Palpimanoidea - Anexo IV

Los palpimanoideos son un grupo muy pequeño de arañas, con unas 200 especies actuales, reconocible por la presencia de unas setas especialmente engrosadas en el margen interno de los quelíceros a modo de dientes, los llamados *peg teeth* (Forster & Platnick, 1984; Platnick, 2012). Las primeras evidencias de la existencia de la superfamilia provienen de yacimientos de compresión del Jurásico de China (Selden et al., 2008). Los registros preexistentes de la superfamilia en el Cretácico se limitaban a varios ejemplares descritos del ámbar de Myanmar, un ejemplar descrito del ámbar de Francia (Archingeay-Les Nouillers) y varios ejemplares del ámbar de Canadá (Penney, 2003; Penney & Selden, 2006; Wunderlich, 2008; Saupe & Selden, 2009). Se han estudiado varios palpimanoideos del ámbar de Peñacerrada I. Todos ellos presentaban una posición filogenética (y consecuente asignación taxonómica) incierta debido al precario conocimiento de la filogenia y límites internos de la superfamilia (véase Forster & Platnick, 1984). Es por ello que, para disponer de criterios de peso con los que clasificar los nuevos fósiles (y aquellos que habían sido previamente descritos) dentro de una filogenia general del grupo, se vio necesario llevar a cabo un análisis filogenético de la superfamilia Palpimanoidea, que correspondería al primer intento de incorporar palpimanoideos actuales y fósiles en una filogenia (anexo IV; Saupe et al., 2011; Wood et al., 2012). Actualmente, los palpimanoideos presentan distribuciones eminentemente australes relativamente confinadas (salvo la familia Palpimanidae, también con presencia en el Mediterráneo y Asia Central) (Forster & Platnick, 1984). No obstante, los nuevos hallazgos sugieren que el grupo se hallaba bien diversificado en el Hemisferio Norte durante el Cretácico, algo que había sido anteriormente apuntado (Penney & Selden, 2006; Selden et al, 2008).

B.1.1.1. F. †Lagonomegopidae Eskov & Wunderlich, 1994 - Pérez-de la Fuente et al. (2012d, *en prensa*): anexo I.10

Los lagonomegópidos son unas arañas estrictamente cretácicas. Se considera que pertenecen a la superfamilia Palpimanoidea, si bien sus relaciones filogenéticas no han sido del todo resueltas. El grupo se reconoce por la presencia de un par de ojos (*ops*) especialmente agrandados (*mega*) en posición anterolateral (*lagono* = flanco) del prosoma. Aunque su biología sigue siendo un misterio, se cree que, al igual que el resto de palpimanoideos, eran arañas merodeadoras y, por tanto, no usaban telarañas como medio de captura de presas. Se conocían seis especies descritas en cuatro géneros, procedentes de los ámbares de Jordania, España, Myanmar, EUA (Nueva Jersey), Federación de Rusia (Taimyr) y Canadá (Eskov & Wunderlich, 1995; Penney, 2002, 2004, 2005, 2006a). El nuevo material español amplía esta diversidad en dos nuevos géneros, uno monoespecífico y otro con dos especies diferenciadas, y una nueva especie de un género previamente conocido. En El Soplao, el grupo queda representado por el nuevo género y especie *Soplaogonomegops unzuei* Pérez-de la Fuente, Saupe & Selden, 2012 (CES 362). La presencia de un largo cuello prosómico en este taxón, tal y como típicamente sucede en los palpimanoideos de la familia Archaeidae Koch & Berendt, 1854, así como otros caracteres presentes en los otros nuevos taxones españoles (anexo III), refuerza la asignación de la familia †Lagonomegopidae a Palpimanoidea. Por otra parte, otro lagonomegópido (CES 408) es asignable al género †*Lagonomegops* Eskov & Wunderlich, 1994.

El nuevo material del ámbar de España ha permitido la sinonimización de la familia †Grandoculidae Penney, 2011, creada a partir de *Grandoculus chemahawinensis* Penney, 2004 procedente del ámbar de Canadá, con †Lagonomegopidae (Penney, 2011).

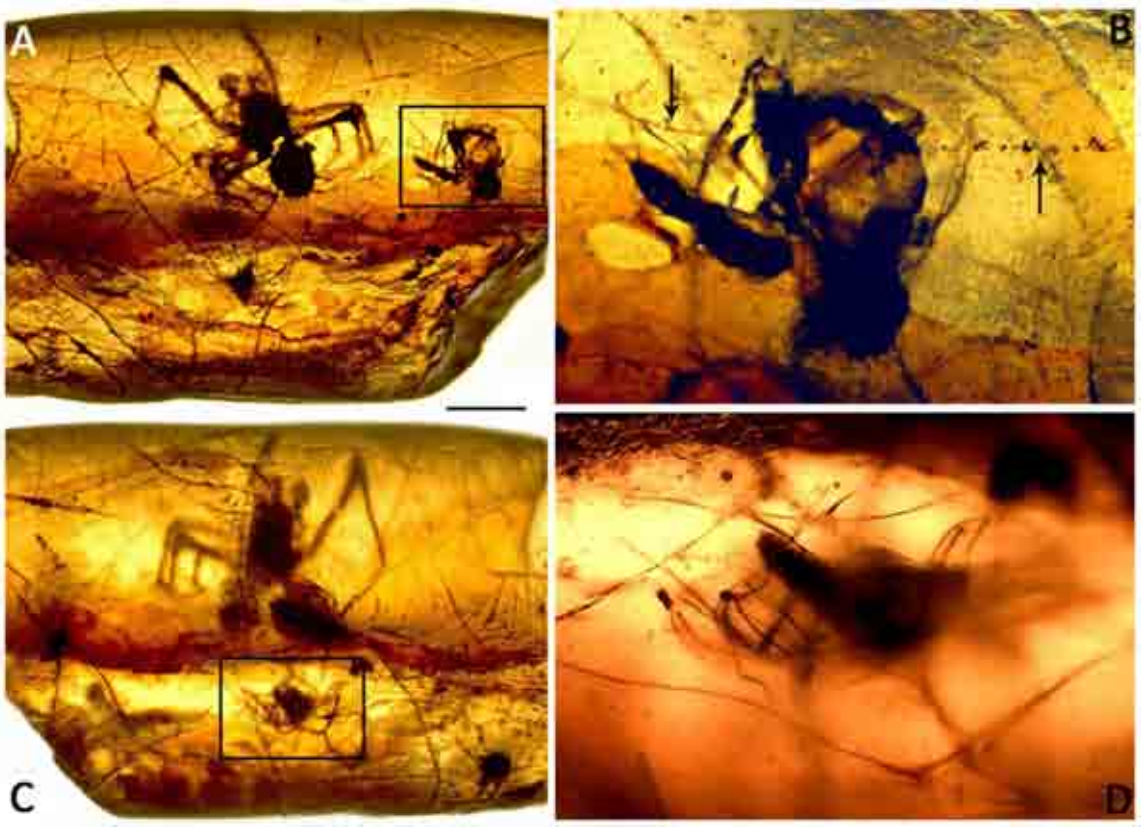
B.1.2. Superf. Dysderoidea: F. Oonopidae Simon, 1890 - Saupe et al. (2012): anexo I.9

Los oonópidos son diminutas arañas nocturnas merodeadoras representadas por unas 450 especies actuales de distribución mundial (Jocqué & Dippenaar-Schoeman, 2006). Viven en hábitats muy variados, por ejemplo bajo la corteza de los árboles, en el suelo, entre el follaje y en las telarañas de otras arañas (Saaristo, 2001). Aunque no se conocen fósiles de compresión/impresión, probablemente debido a su pequeño tamaño (Penney & Selden, 2011), la familia es de las más abundantes en ámbar y ha sido hallada en más depósitos que ninguna otra, con registro previamente conocido en los ámbares cretácicos del Líbano, Myanmar, EUA (Nueva Jersey) y Canadá (Penney, 2006b). La especie descrita de El Soplao pertenece al género *Orchestina* Simon, 1882. Este género de oonópidos, con una treintena de especies fósiles descritas, es el más común de la familia en el registro fósil (Dunlop et al., 2011), y también el más ancestral. En este sentido, la nueva especie descrita a partir del registro El Soplao, *Orchestina rabagensis* Saupe, Pérez-de la Fuente, Selden, Delclòs, Tafforeau & Soriano, 2012 (CES 013), corresponde actualmente al taxón más antiguo de la familia. El único ejemplar hallado corresponde a un macho; sólo los de este sexo poseen los caracteres diagnósticos (en los pedipalpos) para diferenciar especies, un hecho común en la taxonomía de arácnidos. Los otros dos ejemplares descritos del ámbar de España son hembras, y el procedente de San Just fue descrito en detalle gracias al uso de las técnicas de la luz de sincrotrón (Soriano et al., 2010: anexo I.4).

B.1.3. *Telarañas*

Las telas de araña presentan una gran diversidad en composición y estructura (Vollrath & Selden, 2007). Es por ello que a través del estudio de las mismas como inclusiones en ámbar se puede llegar a inferir la existencia de ciertos grupos ecológicos de arañas aunque, quizá por causas tafonómicas, no se tenga registro de las arañas productoras. Asimismo, las telarañas tienen el potencial de proporcionar una valiosa información paleoecológica por poseer un elevado carácter etológico (ibid.), además de reflejar el estrecho vínculo evolutivo de las arañas con sus presas mayoritarias, los insectos (Peñalver et al., 2006b). Han sido estudiadas numerosas muestras de telarañas procedentes de los tres yacimientos principales de ámbar españoles. En El Soplao, las muestras en las que se han detectado inclusiones de telarañas son: CES 057, 315, 373, 378, 379, 403, 410 y 476 (no se muestran en el listado proporcionado en el anexo II ya que sólo recoge las macrobioinclusiones). La pieza de ámbar correspondiente a la muestra CES 476 tiene una morfología de tipo estalactita y es especialmente singular al preservar junto al resto de telaraña la supuesta araña productora (un posible araneido), un posible rafidióptero, un neuróptero coniopterígido, dos himenópteros (uno de ellos un platigástrido) y un díptero. Algunos de ellos se encuentran atrapados por hebras de la telaraña (Fig. 33). La asociación fósil, como sininclusiones, de un potencial depredador, el mecanismo de caza y las presas representa un hecho muy excepcional en Paleontología. No obstante, ciertos micelios de hongos conservados en ámbar pueden ser fácilmente malinterpretados

como restos de telarañas. El grueso del filamento y la variación del mismo, así como la conformación espacial que varios filamentos pueden adoptar entre sí, son criterios relevantes. Se ha indicado que la presencia de diminutas gotas adhesivas en un filamento indica su origen en la parte espiral de una tela orbicular (Zschokke, 2003; Foelix, 2011). Criterios que sugieren la naturaleza fúngica del filamento son la presencia de fructificaciones o la existencia de un halo en torno al filamento, que corresponde a una alteración en la composición de la resina en las primeras fases bioestratinómicas debido a la acción de sustancias derivadas del metabolismo fúngico. Cabe señalar que los análisis en microscopía confocal de fluorescencia (apartado 3.3.2; Speranza et al., 2010) que se llevaron a cabo sobre estas muestras no fueron concluyentes, ya que no se detectó señal de excitación que permitiera reconocer compuestos fúngicos en los filamentos. Por ello, se continúa con la determinación de un mayor número de criterios morfológicos para discernir el origen de una gran parte de estas estructuras filamentosas. La aplicación de los criterios antes mencionados ha llevado a considerar que muchos de los registros descritos anteriormente en la bibliografía como telarañas podrían corresponder a hifas fúngicas (véase por ejemplo Wunderlich, 2004: fotografía 549).



▲ **Fig. 33.** Pieza con forma de estalactita en el ámbar de El Soplao con una araña, una telaraña y tres presas atrapadas (un díptero, un himenóptero y un neuróptero). **A**. Vista general de la pieza. La zona enmarcada se muestra aumentada en B. **B**. Díptero e himenóptero platigástrido atrapados por una hebra de telaraña (flechas). **C**. Vista general de la pieza por el lado opuesto al mostrado en A. La zona enmarcada se muestra aumentada en la figura D. **D**. Coniopterígido (Neuroptera) atrapado entre hebras de telaraña con disposición en red. Escala = 1 mm (A y C con la misma escala).

B.2. "SUBCL. ACARI"

Las filogenias actuales tienden a considerar a los ácaros como una agrupación no natural, reconociendo a los grupos de ácaros acariformes y ácaros parasitiformes como linajes independientes (Dunlop & Penney, 2012). El registro de ácaros acariformes se remonta hasta el Devónico Inferior, mientras que el de ácaros parasitiformes hasta el Cretácico.

B.2.1. SUPERO. ACARIFORMES

B.2.1.1. O. TROMBIDIFORMES

B.2.1.1.1. F. Erythraeidae Robineau-Desvoidy, 1828

Las formas larvarias de esta familia son ectoparásitos de otros artrópodos, mientras que las formas adultas son depredadores de vida libre (Krantz & Walter, 2009). Se han reconocido tres ejemplares pertenecientes a esta familia (CES 389.5, 530.18 y 598.1); los dos primeros se han asignado al género *Leptus* Latreille, 1796 (Fig. 34A). El grupo ha sido hallado en los ámbares cretácicos de España (Peñacerrada I), Myanmar y Canadá (Grimaldi et al., 2002; McKellar & Wolfe, 2010; Peñalver & Delclòs, 2010).

B.2.1.1.2. F. Bdellidae Dugès, 1834

Los miembros de esta familia son activos depredadores que viven en el suelo o en la vegetación, cazando mayormente colémbolos u otros ácaros (Gerson et al., 2003). En El Soplao se ha hallado un ejemplar de bdéllido (CES 366; Fig. 34B). Hasta la fecha, los registros fósiles de la familia se limitaban a una especie del ámbar de Canadá y cuatro especies del ámbar del Báltico (Ewing, 1937; Koch & Berendt, 1854; Dunlop et al., 2011), aunque también se han reconocido en el ámbar de Myanmar (Grimaldi et al., 2002). Actualmente, el ejemplar se halla en proceso de estudio por los Drs. Antonio Arillo y Eduard Ueckermann, quienes han apuntado que el fósil podría asignarse al género *Spinibdella* Thor, 1930.

B.2.1.2. O. SARCOPTIFORMES: SubO. Oribatida

Los oribátidos son ácaros sin formas parásitas conocidas, eminentemente edáficos aunque también con formas arborícolas, saxícolas e incluso acuáticas, de hábitos detritívoros o fitófagos (Krantz & Walter, 2009). Se han reconocido ejemplares pertenecientes a las tres familias siguientes.

B.2.1.2.1. F. Neoliodidae Sellnick, 1928

Esta familia tiene una distribución cosmopolita y cuenta con unas 50 especies actuales conocidas que se reparten en cuatro géneros (Subías, 2012). Se ha reconocido un ejemplar (CES 582) que podría corresponder al género *Platyliodes* Berlese, 1917, ácaros eminentemente asociados a musgos (ibid.). Representantes fósiles del grupo han sido anteriormente reconocidos y descritos en los ámbares cenozoicos del Báltico, República Dominicana y Méjico (Chiapas) (Dunlop et al., 2011), por lo que la aparición de la familia se incrementaría en unos 70 millones de años.

B.2.1.2.2. F. Nothridae Berlese, 1896

Esta familia de oribátidos había sido descrita como fósil anteriormente sólo del ámbar eoceno del Báltico (Dunlop et al., 2011). El ejemplar de El Soplao (CES 505) se clasifica en el género *Nothrus* Koch, 1836, y posee características que lo acercan a las especies tropicales del género. Las especies de este género se hallan asociadas a hojarasca o césped (Subías, 2012).

B.2.1.2.3. F. Trhypochthoniidae Willmann, 1931

Esta familia de oribátidos presenta actualmente unas 50 especies repartidas en ocho géneros de distribución cosmopolita (Subías, 2012). Se ha reconocido un ejemplar (CES 412) que se clasifica dentro del género *Afronothrus* Wallwork, 1961, con especies actuales de afinidad tropical que viven mayoritariamente en hojarasca muy variada (Wang et al., 1999). La diversidad fósil descrita del género proviene de fósiles en compresión del Jurásico de la Federación de Rusia, el ámbar de España (Peñacerrada I), y los ámbares cenozoicos del Báltico y República Dominicana (Dunlop et al., 2011; Arillo et al., 2012).

B.2.2. SUPERO. PARASITIFORMES: O. IXODIDA: F. Argasidae Koch, 1844

El ejemplar único hallado en El Soplao corresponde a lo que comúnmente se denomina garrapata blanda (CES 530.17; Fig. 34C), familia Argasidae. Esta familia cuenta actualmente con unas 200 especies (Guglielmone et al., 2010). Tan sólo tres representantes fósiles del grupo han sido reconocidos hasta la fecha, dos de ellos descritos, en los ámbares cretácicos de Myanmar y de EUA (Nueva Jersey), y del Mioceno de la República Dominicana (Poinar, 1985; Klompen & Grimaldi, 2001; Dunlop et al., 2011; Shi et al., 2012). Por tanto, el ejemplar de El Soplao corresponde al registro más antiguo de la familia y de hecho del superorden Parasitiformes en su totalidad (véase Dunlop & Penney, 2012). Los argásidos, como todos los ixódidos y al igual que sus parientes, las garrapatas duras, son ectoparásitos que se alimentan de la sangre de vertebrados, tales como aves y mamíferos.

6.3.3. SUBFILO CRUSTACEA: CL. MALACOSTRACA: O. TANAIDACEA

Tres especies pertenecientes a este grupo de pequeños crustáceos que habitan aguas salobres o marinas fueron ya descritas del ámbar de Peñacerrada I, estableciéndose una nueva familia, †Alavatanaidae Vonk & Schram, 2007. Su existencia es indicativa de la proximidad de la paleolínea de costa a las plantas emisoras de resina (Vonk & Schram, 2007). El ejemplar de El Soplao (CES 380, Fig. 34D) representa presumiblemente un nuevo morfotipo de estos tanaidáceos. La presencia de estos crustáceos en el ámbar de El Soplao es un indicativo más que apoya unas características paleoecológicas similares para los yacimientos españoles. Los tanaidáceos son muy escasos en ámbar; tan sólo se conocen otros registros en los ámbares franceses de Archingeay-Les Nouillers, La Buzinie y Fortou (Perrichot et al., 2007), todos del Cretácico (Albiense-Cenomaniense).

▲ **Fig. 34**. Ácaros (Arachnida) y crustáceos del ámbar de El Soplao. **A**. Ácaro inmaduro perteneciente al género *Leptus* (Erythraeidae), CES 530.18. **B**. Ácaro perteneciente a la familia Bdellidae, CES 366. **C**. Ácaro perteneciente a la familia Argasidae, comúnmente denominadas garrapatas blandas, CES 530.17. **D**. Crustáceo tanaidáceo (Malacostraca: Tanaidaceae), CES 380. Escalas: A, B = 0,2 mm; C, D = 0,5 mm. Fotografía B por Rafael López del Valle.

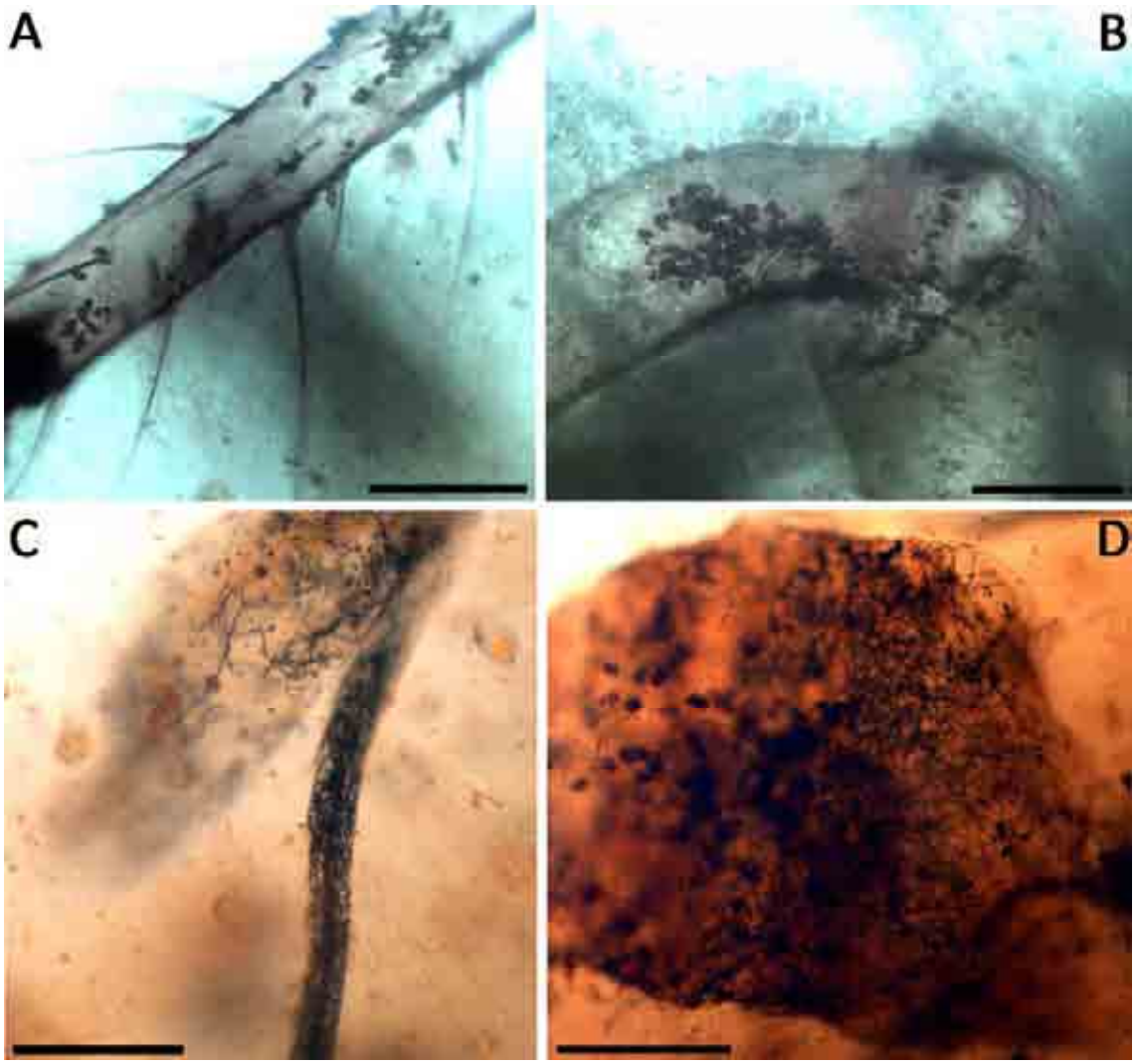
6.4. Bioinclusiones no artropodianas

Se detallan brevemente a continuación otras inclusiones, de origen no artropodiano, que completan la asociación de fósiles hallada en el ámbar de El Soplao. Dichas inclusiones no constan en el listado proporcionado en el anexo II por no corresponder a macrobioinclusiones de artrópodos.

6.4.1. Microbioinclusiones

La preservación de microorganismos en ámbar, ésto es, bacterias, protozoos, hongos e incluso algas, es abundante y bien conocida (por ej., Breton & Tostain, 2005; Girard et al., 2009; Speranza et al., 2010), si bien en algunos casos algunos su verdadera naturaleza es controvertida (Girard et al., 2011). Están también presentes en el ámbar de El Soplao, pero su estudio no ha sido un objetivo de este proyecto de Tesis Doctoral. Aun así, por su relación con las inclusiones de artrópodos, cabe resaltar algunas inclusiones de insectos con hongos asociados. El holotipo de *Necroraphidia arcuata* se halla asociado a hifas ubicadas en el abdomen y venación alar del insecto, sobre todo en las venas costales y subcostales (Pérez-de

la Fuente et al., 2012a: fig. 4, anexo I.6). Por otra parte, en el nuevo morfotipo de larva de crisopoideo (CES 418; apartado A.8.2.1) existen esporas fúngicas binucleadas que forman agregados internos en el cuerpo del insecto (Fig. 35A, B). Finalmente, el cuerpo de un himenóptero (CES 364.3) se halla casi en su totalidad relleno de hifas que conforman un denso micelio. Presumiblemente debido a la actividad fúngica, la cutícula del insecto está muy degradada y casi no se ha preservado. Por ello, el conjunto de hifas representa un molde interno del cuerpo del insecto (Fig. 35C, D). El estudio de los hongos del ámbar de El Soplao se lleva a cabo en colaboración con la Dra. Mariela Speranza.



▲ **Fig. 35**. Muestras con inclusiones fúngicas del ámbar de El Soplao. **A–B**. Nuevo morfotipo de larva de neuróptero crisopoideo, CES 418. A. Parte de la tibia derecha. Nótense los agregados de esporas binucleadas. B. Articulación femorotibial. Nótense los agregados de esporas binucleadas. **C–D**. Hymenoptera indeterminado, CES 364.3. C. Vista de una tibia. D. Vista de la cara ventral de la parte proximal del abdomen. Escalas: A, B, C = 0,1 mm; D = 0,2 mm.

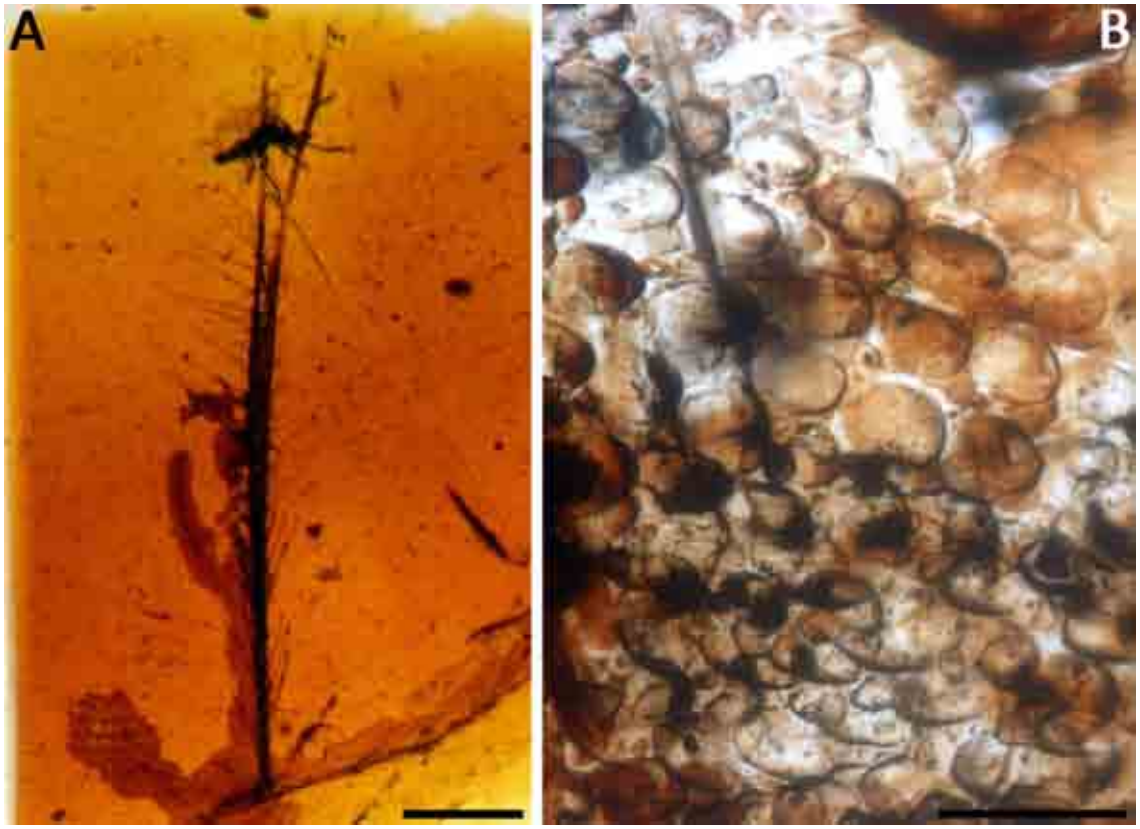
6.4.2. Plantas

Como inclusiones de plantas indicar restos foliares (CES 371.2 y 378) y otros restos de plantas indeterminados (CES 475), algunos de ellos con forma de simples fibras (CES 486,

Pérez-de la Fuente et al., 2012a: fig. 12, anexo I.6). Además, es la primera vez que han sido descritos fragmentos de fusinita como inclusiones en ámbar (Najarro et al., 2010: fig. 7.1, anexo I.2; Pérez-de la Fuente et al., 2012a: figs 4A, 7A, anexo I.6). Por último, apuntar la existencia de varias muestras con tricomas, además de los que constituyen la agrupación que conforma el *trash packet* que fue recolectado por el nuevo morfotipo de larva de crisopoideo (véase el apartado A.8.2.1; Pérez-de la Fuente et al., 2012e, *reenviado a la revista tras informe favorable de revisores*: anexo I.11).

6.4.3. Vertebrados

Las evidencias de vertebrados en ámbar, tanto del Mesozoico como del Cenozoico, son muy escasas. En El Soplao han aparecido dos restos de plumas y uno de piel de reptil. Las dos muestras identificadas como plumas, CES 426.1 y 457.1, no han sido estudiadas por ahora y podrían corresponder a dinosaurios terópodos no avianos o a aves primitivas (dinosaurios avianos) (Fig. 36A). Otras asociaciones de plumas han sido estudiadas en los ámbares de Francia (Archingeay-Les Nouillers) (Perrichot et al., 2008) y Canadá (McKellar et al., 2011). Asimismo, existe constancia de plumas en otros ámbares españoles (Peñacerrada I y San Just) y en los ámbares del Líbano, Myanmar, EUA (Nueva Jersey) y Federación de Rusia (Taimyr) (Schlee, 1973; Kurochkin, 1985; Grimaldi & Case, 1995; Alonso et al., 2000; Grimaldi et al., 2002; Peñalver & Delclòs, 2010). El registro de otros restos de vertebrados que no sean plumas



▲ **Fig. 36**. Inclusiones pertenecientes a vertebrados en el ámbar de El Soplao. **A**. Resto de pluma perteneciente a dinosaurio terópodo no aviano o a ave primitiva. **B**. Detalle del patrón de disposición de las escamas epidérmicas de un fragmento de piel de reptil, seguramente una muda. Escalas = 0,5 mm. Fotografía A por Rafael López del Valle.

es aún muchísimo más escaso. En El Soplao ha aparecido un pequeño resto de piel de reptil (CES 541), que por su preservación correspondería a un pequeño fragmento de una muda (Fig. 36B). El resto de reptil más completo que ha aparecido en ámbar cretácico es un fragmento de piel y pata con uñas preservados del ámbar del Líbano (Arnold et al., 2002). Restos similares al del ámbar de El Soplao han sido descritos del ámbar de Myanmar y de Francia (Archingeay-Les Nouillers), correspondiendo a uno y a dos restos de piel, respectivamente (Grimaldi et al., 2002; Perrichot & Néraudeau, 2005). Estos últimos fueron atribuidos a un escamoso (orden Squamata) de pequeño tamaño, como un lagarto. No se encuentran registros similares hasta el Eoceno del ámbar del Báltico (Weitschat & Wichard, 2002, 2010). La inclusión de El Soplao corresponde al primer registro de reptil en ámbar de España.

7. DISCUSIÓN

7.1. Tafonomía y reconstrucción paleoambiental

Los datos paleobiológicos generados durante la confección de la presente Tesis Doctoral, relativos al ámbar de El Soplao y sus bioinclusiones, han complementado los datos tafonómicos y de reconstrucción paleoambiental que la geología y los restos paleontológicos asociados al ámbar habían proporcionado previamente (véase Najarro et al., 2009: anexo I.1).

En el yacimiento de El Soplao existe una gran abundancia de piezas de ámbar frágiles (Fig. 20), que no hubieran resistido un transporte intenso o prolongado. Además, acompañando a las piezas de ámbar se hallan tallos vegetativos de †*Frenelopsis* en conexión anatómica (Fig. 19A; Najarro et al., 2010: anexo I.2), raíces *in situ* (Fig. 19B) y rizocreciones (Fig. 19C). Todo ello indica que la resina apenas sufrió transporte, o muy poco, desde que fue secretada hasta su enterramiento, y que por tanto la acumulación de resina que dio lugar al yacimiento de El Soplao tuvo un origen paraautóctono. El establecimiento de la parautoctonía del yacimiento de El Soplao representa el punto de partida para la extracción de inferencias paleoecológicas fidedignas.

El agente principal que habría promovido la secreción y posterior acumulación de resina que dio lugar al yacimiento de ámbar de El Soplao son los incendios (apartado 2.2: hipótesis 5). Las evidencias paleobiológicas que señalan a los paleoincendios son tres. La primera evidencia, y prueba más directa de ello, es la abundancia de materia vegetal fusinizada asociada al ámbar (apartado 4.2.2), así como la existencia de fibras vegetales funisizadas como inclusiones en ámbar (apartado 6.4.2; Najarro et al., 2010: anexo I.2; Pérez-de la Fuente et al., 2012a,b: anexos I.6 y I.7). La segunda evidencia es la especial abundancia de rafidiópteros (mesorafídidos), que pudiera deberse a la disponibilidad de mucha madera debido al efecto de los paleoincendios. Esta disponibilidad pudo favorecer a las poblaciones de organismos xilófagos o xilófilos, entre estas últimas las poblaciones de mesorafídidos (apartado A.7; Pérez-de la Fuente et al. 2012a: anexo I.6). Por último, la afinidad del *trash packet* del nuevo morfotipo de larva de neuróptero crisopoideo con los helechos de la familia Gleicheniaceae guarda relación con los paleoincendios, ya que este grupo de helechos, desde el Jurásico Superior, es un colonizador pionero de ambientes alterados por incendios o erupciones volcánicas (apartado A.8.2.1; Pérez-de la Fuente et al., 2012e, *reenviado a la revista tras informe favorable de revisores*: anexo I.11). Estos dos últimos casos se relacionan con la hipótesis 5 del apartado 2.2. Unos posibles promotores adicionales de la secreción de resina en El Soplao hubieran sido grupos de insectos con hábitos barrenadores de madera (apartado 2.2: hipótesis 8). Entre estos grupos destacan los escarabajos pertenecientes a la superfamilia Curculionoidea (apartado A.9.2.4; Najarro et al., 2010: anexo I.2).

Existen bioinclusiones que indican que la resina secretada hubiera presentado una alta fluidez. El ejemplo más representativo es la intrincada nube de tricomas que conforma el *trash packet* del nuevo morfotipo de larva de neuróptero crisopoideo (apartado A.8.2.1; Pérez-de la Fuente et al., 2012e, *reenviado a la revista tras informe favorable de revisores*: anexo I.11), el

cual no hubiera podido quedar englobado por la resina de un modo tan homogéneo, sin la formación de burbujas, de no ser por un alto grado de fluidez de la resina en el momento de inclusión.

La presencia en El Soplao del género de ceratopogónidos *Austroconops* (apartado A.12.1.1.1; Pérez-de la Fuente et al., 2011: anexo I.5), del género de dolicopódidos †*Cretomicrophorus* (apartado A.12.2.3.1.3) y de un crustáceo tanaidáceo (apartado 6.3.3) sugieren la cercanía de las fuentes emisoras de resina que dieron lugar al yacimiento de El Soplao a la línea de paleocosta. Otras evidencias de ello, tras constatar la paraauctoctonía del yacimiento, son fósiles de moluscos marinos o de agua salobre que se encuentran asociados al ámbar (apartado 4.2.3) y algunas piezas de ámbar colonizadas por briozoos y serpúlidos (apartado 4.2.3; Najarro et al., 2010: anexo I.2), hecho que demuestra que presentaron un periodo relativamente largo de exposición en aguas salobres o marinas antes de ser enterradas definitivamente (contrástese con la hipótesis 4 del apartado 2.2).

7.2. Comparación paleofaunística

A continuación se compara la paleodiversidad de artrópodos del ámbar de El Soplao con la de los ámbares cretácicos principales (véase entradas en negrita de la Tabla 1). Ello guarda relación con las hipótesis 2, 3 y 7 mostradas en el apartado 2.2. El número de ejemplares (549 en total, véase el apartado 6.2) es aún limitado, y por ello todas las ideas extraídas a partir de la abundancia relativa de los distintos grupos han de tomarse teniendo este hecho en consideración.

Uno de los rasgos más distintivos del ámbar de El Soplao es que el grupo de los himenópteros es el predominante (véase el apartado 6.2). Esto contrasta con la mayoría de ámbares cretácicos principales, en los que predomina el grupo de los dípteros (Tabla 4). Además de los ámbares mostrados en la Tabla 4, aquellos más similares en edad al ámbar de El Soplao, los dípteros son también mayoritarios en el ámbar de Nueva Jersey, representando alrededor del 30% del total de inclusiones (Grimaldi & Nascimbene, 2010). Según McKellar & Wolfe (2010), no existen datos de abundancia fiables para el ámbar de Canadá por el sesgo que supone haber estudiado algunos grupos más intensamente que otros.

El linaje de himenópteros más común en los ámbares cretácicos es el de los proctotrupomorfos, y en El Soplao esto no es una excepción. Su pequeño tamaño y su baja capacidad voladora son las causas tafonómicas principales que explican este sesgo (apartado 5.1.1). En este sentido, el grupo de himenópteros, y por tanto de artrópodos, más abundante es el de los platigástridos (apartado A.10.1.3.2), que representa un 40,4% del total de himenópteros y un 16,9% del total de macrobioinclusiones (apartado 6.2: Tabla 3). Tal preponderancia, aunque en mucha menor proporción que en El Soplao, se manifiesta en los ámbares cretácicos principales (Ortega-Blanco, 2010; McKellar & Engel, 2012). Otros proctotrupomorfos, como los serfítidos y los mimarommátidos (apartado A.10.1.3.1), tienen un registro similar al de la mayoría de ámbares cretácicos principales (véase Ortega-Blanco et al., 2011a,b; Engel et al., 2011).

Grupos aparecidos en El Soplao	El Soplao	Peñ.	Arc.	Ham.	Mya.*
Hymenoptera	42,51	24,69	17,39	6	8,69
Diptera	23,66	40,72	43,65	51,11	33,7
Coleoptera	9,43	3,13	4,26	3,26	15,95
Thysanoptera	4,44	3,63	0,25	3,23	5,06
Psocodea	3,14	4,14	3,26	2,82	2,67
Hemiptera	2,96	6,15	4,52	17,75	7,43
Araneae	2,96	2,57	3,35	1,18	3,87
"Acari"	2,96	2,89	7,78	8,61	8,86
Neuroptera	2,59	0,86	0,75	0,52	1,05
Raphidioptera	1,85	0,15	0,25	-	0,12
"Blattaria"	1,29	2,72	4,35	2,74	2,77
Lepidoptera	0,92	1,31	1,17	0,88	0,29
Collembola	0,56	4,03	1,51	0,52	2,6
Isoptera	0,37	0,5	0,42	0,39	2,36
Mecoptera	0,18	-	-	-	A
Tanaidacea	0,18	0,71	0,92	-	-
Grupos no aparecidos en El Soplao	**El Soplao**	**Peñ.**	**Arc.**	**Ham.**	**Mya.***
Orthoptera	-	0,6	1,09	-	A
Isopoda	-	0,5	2,93	0,26	0,19
Trichoptera	-	0,26	0,08	0,26	0,41
Archaeognatha	-	0,2	-	0,07	0,12
Plecoptera	-	0,15	-	-	0,05
Pseudoscorpionida	-	0,1	0,25	0,07	1,17
Strepsiptera	-	-	0,5	-	A
Myriapoda	-	-	0,5	0,07	1,79
Dermaptera	-	-	0,42	0,11	0,17
Cladocera	-	-	0,08	-	-
Mantodea	-	-	0,08	-	0,14
Odonata	-	-	0,08	-	0,07
Scorpionida	-	-	0,08	-	0,1
Thysanura	-	-	0,08	0,04	0,1
Ephemeroptera	-	-	-	0,11	0,1
Zoraptera	-	-	-	-	0,1
Embioptera	-	-	-	-	0,07
n	**541**	**~2200**	**1196**	**~3000**	**4187**

▲**Tabla 4.** Comparación de los datos de abundancia relativa de los distintos órdenes de artrópodos aparecidos en el ámbar de El Soplao y los cuatro ámbares principales de edades más similares a éste de los que existen datos de abundancia. El total de bioinclusiones de artrópodos para cada yacimiento (= *n*) no tiene en cuenta los artrópodos indeterminados. Datos de abundancia de grupos de artrópodos extraídos de: Peñ. (Peñacerrada I) - Delclòs et al. (2007), Arc. (Archingeay-Les Nouillers, Francia) - Perrichot et al. (2010), Ham. (Hammana, Líbano) - Azar et al. (2010a), Mya. (Myanmar) - Grimaldi et al. (2002). A: Grupos aparecidos en el ámbar de Myanmar *sensu* Ross et al. (2010). *Colecciones del NHML y AMNH unidas.

Por otra parte, la total ausencia de hormigas en el ámbar de El Soplao (y en el de España en general), sí presentes en los ámbares de Myanmar y Francia, es notable y viene a apoyar las conclusiones extraídas tras el estudio de los himenópteros del ámbar de España por Ortega-Blanco (2010). Se ha visto que, además de por posibles causas tafonómicas, esta diferencia tan singular entre faunas cretácicas tan cercanas en el espacio y en el tiempo como son la española y la francesa se explica por un proceso muy rápido de diversificación de las hormigas a partir del Albiense Superior, o porque las hormigas no habitaron la Placa Ibérica durante el Albiense por el aislamiento de ésta respecto al resto de Laurasia (contrástese con la hipótesis 1 del apartado 2.2). Por el contrario, la familia de proctotrupomorfos †Stigmaphronidae está ausente del ámbar de Francia pero es diversa en el ámbar de España, sobre todo en Peñacerrada I, y también tiene registro en El Soplao (apartado A.10.1.3.3). Por otra parte, la descripción de una nueva especie perteneciente al género de evánidos †*Cretevania* en El Soplao incrementa aún más la especial diversidad de este género en el ámbar de España (apartado A.10.1.2; Pérez-de la Fuente et al., 2012c: anexo I.8).

Respecto a los dípteros, si bien las proporciones entre nematóceros y braquíceros son bastante similares, los primeros abundan algo más. El grupo de los ceratopogónidos (apartado A.12.1.1.1) representa un tercio del total de dípteros y un 7,8% del total de macrobioinclusiones de artrópodos en El Soplao (apartado 6.2: Tabla 3), siendo el grupo más abundante de dípteros y el segundo grupo de artrópodos más abundante, tras los himenópteros platigástridos. Esta predominancia también se da en el resto de yacimientos Cretácicos (Grimaldi & Engel, 2005) y se relaciona a un sesgo tafonómico debido a la cercanía ecológica de los ceratopogónidos a las fuentes de resina, su pequeño tamaño y sus hábitos de enjambramiento (véase el apartado 5.1.1). La menor proporción total de dípteros en El Soplao viene propiciada por la escasez del resto de nematóceros, los cuales sí suelen aparecer de un modo más abundante en el resto de ámbares cretácicos. Estos otros nematóceros son los quironómidos, psicódidos y cecidómidos, que están presentes en menor proporción en el ámbar de El Soplao. En relación a los dípteros braquíceros, su diversidad es elevada y las proporciones de los distintos grupos están dentro de los parámetros habituales en los ámbares cretácicos. Esto último tiene como excepción la sobreabundancia relativa de familia Dolichopodidae en el ámbar de Archingeay-Les Nouillers, que representa alrededor de un 6% del total de inclusiones (Perrichot et al., 2007) y que pudiera denotar una mayor influencia marina del área en la que tuvo lugar el enterramiento de resina que dio lugar al yacimiento. En este ámbar francés también se han hallado microbioinclusiones pertenecientes a organismos marinos (Girard et al., 2009).

El porcentaje de coleópteros es relativamente elevado en El Soplao comparado con los ámbares del Líbano (Hammana), otros ámbares de España (Peñacerrada I) y Francia (Archingeay-Les Nouillers), aunque no llega a los valores tan elevados mostrados por el ámbar de Myanmar (Tabla 4). Por el contrario, el porcentaje de hemípteros está muy por debajo de otros ámbares y lejos de las proporciones del ámbar del Líbano (Hammana) y también de EUA (Nueva Jersey) (Grimaldi & Nascimbene, 2010). Esto último viene propiciado por una baja proporción de coccoideos (o "cochinillas"), que en los ámbares del Líbano, Peñacerrada I, Myanmar y EUA (Nueva Jersey) son comunes (Azar, 2000; Grimaldi et al., 2002; Delclòs et al.,

2007; Grimaldi & Nascimbene, 2010). En los ámbares de Federación de Rusia (Taimyr) y Canadá, los afidoideos son el grupo de hemípteros esternorincos mayoritario, hecho que seguramente refleja una mejor adaptación de este grupo a un clima más estacional (Grimaldi & Engel, 2005).

El ámbar de El Soplao presenta una elevada abundancia relativa de rafidiópteros (Tabla 4; apartado A.7; Pérez-de la Fuente et al., 2012a: anexo I.6). Hay del orden de, al menos, diez veces más rafidiópteros en el ámbar de El Soplao que en el resto de cada uno de los ámbares cretácicos conocidos. La proporción es aún más alta al limitar la comparación a los rafidiópteros adultos, ya que la mayoría de registros en otros ámbares cretácicos corresponden a individuos inmaduros. Su especial abundancia en el ámbar de El Soplao puede deberse a sus hábitos de vida xilófilos y la importancia que los incendios hubieran tenido en la génesis del yacimiento de El Soplao (véase el apartado 7.1). Además, esta abundancia contrasta no sólo con los ámbares Cretácicos principales no españoles sino también con los ámbares de Peñacerrada I y San Just. Por tanto, ello podría indicar algún fenómeno tafonómico o paleofaunístico de tipo local. Asimismo, aunque en menor grado que los rafidiópteros, los neurópteros parecen ser también especialmente abundantes y diversos en El Soplao (Tabla 4; apartado A.8; anexo V).

La presencia de un representante del orden Mecoptera (apartado A.11) es un hecho extremadamente raro, ya que parece que únicamente se han encontrado otros dos ejemplares en ámbar de Myanmar (Grimaldi et al., 2005), pese a que algunos ámbares, como los del Líbano, cuentan con miles de inclusiones (Azar et al., 2010a). Otras inclusiones aún más excepcionales, las cuales se desconocían por completo hasta el momento en el ámbar Cretácico, son las correspondientes al nuevo morfotipo perteneciente a la familia de neurópteros Psychopsidae (apartado A.8.1.2: anexo V); al nuevo morfotipo de larva perteneciente a la superfamilia de neurópteros Chrysopoidea (apartado A.8.2.1; Pérez-de la Fuente et al., 2012e, *reenviado a la revista tras informe favorable de revisores*: anexo I.11); y a los tres ejemplares (dos hembras y un macho preservados como sininclusiones) que conforman un nuevo morfotipo perteneciente a la familia de dípteros †Zhangsolvidae (apartado A.12.2.1).

La diversidad de arácnidos en el ámbar de El Soplao es significativa en tanto en cuanto ha permitido describir la araña de la familia Oonopidae más antigua conocida en la actualidad (apartado B.1.2; Saupe et al., 2012: anexo I.9), así como una araña de la familia †Lagonomegopidae (apartado B.1.1.1; Pérez-de la Fuente et al., 2012d, *en prensa*: anexo I.10) que emparenta estas enigmáticas arañas estrictamente cretácicas con las arañas de la superfamilia Palpimanoidea, la cual tiene un registro relativamente diverso en el ámbar de España (apartado B.1.1, anexo IV). Las telarañas son también abundantes en el registro del ámbar de El Soplao, y existen muestras con especial interés paleoecológico por presentar también las presas atrapadas en la telaraña como sininclusiones o incluso la potencial araña constructora de la misma (apartado 2.2: hipótesis 6; apartado B.1.3). Además, el ámbar de El Soplao ha brindado los primeros registros conocidos de varios grupos de ácaros, ésto es, de la familia de trombidiformes Bdellidae (apartado B.2.1.1.2), de las familias de oribátidos Neoliodidae y Nothridae (apartados B.2.1.2.1 y B.2.1.2.2), y, de forma más notable, del

superorden Parasitiformes, con un ejemplar de "garrapata blanda" (familia Argasidae) (apartado B.2.2).

Varios son los grupos de artrópodos de los que no se tiene registro en El Soplao y que han aparecido en otros ámbares (Tabla 4), aunque su proporción en los mismos, cuando están presentes, es tan baja que su ausencia en el ámbar de El Soplao puede deberse a una cuestión meramente estadística. Cabe destacar la ausencia de ortópteros (grillos y saltamontes), relativamente muy abundantes en el ámbar francés de Archingeay-Les Nouillers, conformando alrededor del 3% del total de inclusiones (Tabla 4). Su abundancia en este yacimiento francés ha sido relacionada a la elevada proporción de piezas de ámbar que habrían preservado fauna edáfica (Perrichot, 2004). Por tanto, su ausencia en El Soplao podría indicar una baja proporción de resina que habría llegado hasta el suelo del bosque atrapando fauna edáfica, hecho que estaría en consonancia con la elevada abundancia constatada de piezas de ámbar de origen aéreo en el yacimiento de El Soplao (Najarro et al., 2009: anexo I.1).

Las tres especies de insectos formalmente descritas que son comunes a El Soplao y Peñacerrada I corresponden a dos himenópteros y un díptero: el megalírido *Megalava truncata* (Perrichot, 2009; Pérez-de la Fuente et al., 2012b: anexo I.7), el mimaromátido *Archaeromma hispanicum* (Ortega-Blanco et al., 2011b) y el ceratopogónido *Protoculicoides skalskii* (Szadziewski & Arillo, 1998; Pérez-de la Fuente et al., 2011: anexo I.5). Esta última especie también aparece en San Just (Arillo et al., 2008b). Cabe además sumar una cuarta especie, un himenóptero plastigástrido, aún no descrita formalmente (Ortega-Blanco, 2010). La correlación de yacimientos usando la paleoentomología ha sido usada por McKellar et al. (2008) para los ámbar de Canadá y por Azar et al. (2010a) para los ámbares del Líbano. En conjunto, estas especies comunes a El Soplao y Peñacerrada I representan una evidencia paleoentomológica que apoya a los datos geológicos y al resto de datos paleobiológicos para ambos yacimientos de la Cuenca Vasco-Cantábrica, los cuales apuntan una edad muy parecida entre ambos. Existen, no obstante, datos geológicos y paleobotánicos que indican diferencias paleoambientales entre ambos yacimientos, con una mayor influencia marina para el yacimiento de El Soplao que para el yacimiento de Peñacerrada I (Peñalver & Delclòs, 2010).

Asimismo, existen evidencias que indican con carácter preliminar la similitud entre las paleofaunas de los ámbares de El Soplao y el Líbano. En El Soplao se han descrito dos nuevas especies de géneros también descritos del ámbar del Líbano pero no conocidos de ningún otro ámbar cretácico. El primero es el ceratopogónido *Lebanoculicoides excantabris.* El género †*Lebanoculicoides* tan sólo había sido descrito anteriormente del ámbar del Líbano (Szadziewski, 1996), y representa el grado más ancestral de la familia Ceratopogonidae (apartado A.12.1.1.1; Pérez-de la Fuente et al., 2011: anexo I.5). El segundo es el tisanóptero *Tethysthrips hispanicus* (apartado A.6; Nel et al., 2010). Esta especie presenta un elevado grado de similitud con la otra especie descrita del género, *T. libanicus*, del ámbar del Líbano (ibid.). También existen casos de similitudes faunísticas exclusivas entre el ámbar del Líbano y Peñacerrada I. Es el caso del género de himenóptero *Libanophron* Ortega-Blanco, Delclòs & Engel, 2011, descrito primero a partir de una especie del ámbar del Líbano (Engel & Grimaldi, 2009) y posteriormente ampliada su diversidad con la descripción de otra especie del ámbar de Peñacerrada I (Ortega-Blanco et al., 2011c).

7.3. Interacciones paleobióticas - Paleoetología

El estudio de las orictocenosis tiene el potencial de indicar relaciones de conespecificidad y dimorfismos sexuales o de informar acerca de las interacciones paleobióticas entre organismos preservados en el ámbar. La presencia de sininclusiones es común en el ámbar de El Soplao (Fig. 7; Najarro et al., 2009: fig. 12D, anexo I.1). Tan sólo un 14% del total de bioinclusiones de El Soplao (79 de las 549) se han preservado aisladas, ésto es, sin ninguna sininclusión. Diez de las piezas de ámbar que se prepararon y que forman parte de la colección contenían originariamente más de diez sininclusiones. El número más elevado de sininclusiones conocido en El Soplao se presenta en una pieza de ámbar con 52 sininclusiones detectadas, aunque la pieza fue dividida en varias preparaciones (véase el anexo II).

La colección de ámbar de El Soplao ha brindado algunas muestras que reflejan interacciones paleobióticas, a menudo con evidencias paleoetológicas directas preservadas. Ello se halla en relación con la hipótesis 2 mostrada en el apartado 2.2. Los dos únicos casos correspondientes a interacciones paleobióticas intraespecíficas en El Soplao se manifiestan en dípteros. El primero de ellos corresponde a posibles casos de enjambramiento por comportamiento gregario, lo que es común en algunos grupos de dípteros. Siete ejemplares pertenecientes al género †*Euliphora* (Phoridae) fueron hallados originariamente en la misma pieza de ámbar aunque fueron divididos en cinco preparaciones para su estudio (apartado A.12.2.3.3). Se conocen casos anteriores de enjambramiento de fóridos en el ámbar de Canadá (Brown & Pike, 1990). Otro posible caso de enjambramiento es el de un nuevo morfotipo de braquícero indeterminado (nueva especie A, anexo II), con cinco ejemplares hallados originalmente como sininclusiones. Por otra parte, dos dípteros ceratopogónidos asignables al género †*Lebanoculicoides* (CES 423.1 + 423.2) se han hallado en posición de cópula (apartado A.12.1.1.1). Pese a que hallar dos artrópodos en cópula en ámbar es algo excepcional, existen varios registros conocidos de cópula en los ámbares cenozoicos del Báltico y República Dominicana (véase Arillo, 2007). No obstante, el único otro registro cretácico equiparable al presente es el de dos ejemplares de la familia de dípteros Scatopsidae en cópula en ámbar del Líbano (Azar et al., 2010a).

Se han hallado varios casos en el ámbar de El Soplao que reflejan interacciones paleobióticas interespecíficas. El primero de ellos corresponde al estudio del nuevo morfotipo de larva de neuróptero crisopoideo y su paquete de basura a base de tricomas afines a los helechos gleicheniáceos (véase el apartado A.8.2.1, Pérez-de la Fuente et al., 2012e, *reenviado a la revista tras informe favorable de revisores*: anexo I.11). Este ejemplar representa un excepcional ejemplo de como el estudio de las inclusiones en ámbar es capaz de contribuir al conocimiento paleoetológico de la fauna cretácica de artrópodos con gran detalle. La información paleoetológica que esta inclusión brinda es doble. Por una parte, representa la prueba directa más antigua conocida del comportamiento del *trash-carrying*. Mediante este comportamiento, las larvas actuales de crisópido seleccionan activamente y transportan materiales exógenos para obtener beneficios defensivos, ésto es, camuflaje y protección física ante sus presas y depredadores. Por otra parte, queda patente una relación planta-insecto, en la que el mecanismo de defensa de la planta es aprovechado por un organismo depredador para su propia defensa. El segundo ejemplo de relación interespecífica corresponde a un

espécimen de díptero quironómido que se encuentra ectoparasitado a nivel proximal del abdomen por un ácaro indeterminado (CES 531.1 + 531.2) (apartado A.12.1.1.2). Los ácaros son los organismos ectoparásitos más comunes en el ámbar, siendo relativamente abundantes en los ámbares cenozoicos del Báltico y República Dominicana, y también existiendo varios casos conocidos en los ámbares cretácicos (Arillo, 2007). En tercer lugar, destacar aquellos grupos en los que se infiere que presentaban hábitos hematófagos, presumiblemente alimentándose de sangre de vertebrados. Este es el caso de los mosquitos ceratopogónidos (apartado A.12.1.1.1., Pérez-de la Fuente et al., 2011: anexo I.5), los mosquitos flebotómidos (apartado A.12.1.2) y el ejemplar de argásido o "garrapata blanda" (apartado B.2.2). Un grupo adicional en el que se dan casos de hematofagia es el de los dípteros de la familia Rhagionidae (apartado A.12.2.2). Por último, indicar la existencia de una pieza de ámbar en la que una telaraña compleja se ha preservado conjuntamente con varias presas atrapadas y la posible araña productora, reflejando pues una posible relación depredador-presa (apartado B.1.3).

8. CONCLUSIONES

Las plantas productoras de resina que dieron origen al ámbar de El Soplao, coníferas pertenecientes al menos a la familia extinta Cheirolepidiaceae y a otro grupo diferente por determinar, se desarrollarían cerca de la costa marina. Los incendios, como parte integrante de la dinámica del ecosistema, tuvieron un papel determinante en la producción y posterior acumulación de resina que dio lugar al yacimiento, provocando la secreción traumática de resina (en la que los insectos barrenadores de madera pudieron haber colaborado) y eliminando la cobertura vegetal del suelo del bosque. Ello facilitó que el agua de escorrentía erosionara el suelo y movilizara la resina depositada primariamente. Esta resina sufrió un corto transporte y se depositó de un modo paraauctóctono en las áreas de enterramiento definitivo, al no existir indicios de reelaboración ni retrabajamiento del ámbar. Estas áreas donde la resina quedó enterrada y fosilizó corresponden a ambientes de marjal costero o de estuario asociado a una llanura deltaica. Algunas masas de resina presentaron un largo periodo de exposición en las aguas salobres o marinas antes de enterrarse.

Pese a hallarse en una fase de estudio inicial, la diversidad identificada de artrópodos en el ámbar de El Soplao es elevada, y en algunas casos ha brindado el registro más antiguo conocido de ciertos taxones. En un total de 549 inclusiones de artrópodos catalogadas, se han determinado 13 órdenes de hexápodos repartidos en unas 40 familias, cuatro órdenes de arácnidos y uno de crustáceos. La paleofauna de artrópodos de El Soplao muestra una serie de singularidades, tanto cuantitativas como cualitativas, en comparación con el resto de paleofaunas conocidas de los ámbares cretácicos.

Desde el punto de vista cuantitativo, y aunque los datos hayan de ser tomados con cautela por la necesidad de aumentar la colección, las abundancias relativas de himenópteros, de rafidiópteros y, en menor grado, de neurópteros en el ámbar de El Soplao son las más elevadas de los ámbares principales de edades más similares al de El Soplao. Por el contrario, las abundancias relativas de dípteros y hemípteros son las menores. A día de hoy, no ha aparecido ningún ortóptero en el ámbar de El Soplao, hecho que podría indicar una baja proporción de resina que hubiera atrapado fauna edáfica y sería acorde con la abundancia de piezas de ámbar de origen aéreo en el yacimiento de El Soplao.

Desde el punto de visto cualitativo, algunos hallazgos del ámbar de El Soplao son excepcionales por su rareza en el registro fósil de ámbar cretácico. Es el caso de los nuevos morfotipos de cuatro grupos de insectos: el neuróptero psicópsido basado en un ejemplar completo, la larva de neuróptero crisopoideo preservada con su paquete de basura, los tres dípteros zhangsólvidos preservados como sininclusiones y, por último, el ejemplar de mecóptero.

Estas singularidades paleofaunísticas tanto a nivel cuantitativo como cualitativo en el ámbar de El Soplao, aparte de los factores tafonómicos y teniendo además en cuenta los hallazgos anteriores en el ámbar de Peñacerrada I, podrían reflejar un cierto carácter endémico de los ecosistemas ibéricos durante el Albiense debido a la insularidad que la Placa Ibérica adquirió en el Jurásico Inferior.

Existen tres especies de insectos comunes a los ámbares de El Soplao y Peñacerrada I (= Moraza). Ello sugiere una edad muy similar para ambos yacimientos de la Cuenca Vasco-Cantábrica. Además, se han advertido ciertas similitudes entre las paleofaunas del ámbar de España (El Soplao y Peñacerrada I) (Albiense) y las del ámbar del Líbano (Barremiense-Aptiense), aunque se hallen espaciadas en el tiempo por varios millones de años. No obstante, es necesario aumentar las colecciones de los ámbares españoles para dar mayor fundamento a estas observaciones, así como revisar las dataciones del ámbar del Líbano.

La elevada proporción de sininclusiones y muestras que brindan información paleoetológica o acerca de interacciones paleobióticas, tanto intraespecíficas como interespecíficas, dan al ámbar de El Soplao un elevado valor paleoecológico. Existen casos de posible enjambramiento, de cópula, de camuflage/defensa, de relación planta-insecto, de parasitismo, de posible hematofagia y de posible relación depredador-presa.

El yacimiento de ámbar de El Soplao, tras considerar todos los datos paleobiológicos que ha proporcionado, es hoy uno de los principales yacimientos españoles de ámbar, y podría convertirse en un referente a nivel mundial si se incrementa considerablemente el volumen de sus colecciones.

En definitiva, el ámbar de El Soplao brinda una oportunidad excepcional para comprender los ecosistemas terrestres del Cretácico de la Península Ibérica.

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ANEXOS

ANEXO I. Publicaciones relativas al presente Proyecto de Tesis Doctoral

I.1. Najarro, M., Peñalver, E., Rosales, I., **Pérez-de la Fuente, R.**, Daviero-Gomez, V., Gomez, B. & Delclòs, X. 2009. Unusual concentration of Early Albian arthropod-bearing amber in the Basque-Cantabrian Basin (El Soplao, Cantabria, Northern Spain): Palaeoenvironmental and palaeobiological implications. *Geologica Acta* 7(3): 363-387.

I.2. Najarro, M., Peñalver, E., **Pérez-de la Fuente, R.**, Ortega-Blanco, J., Menor-Salván, C., Barrón, E., Soriano, C., Rosales, I., López del Valle, R., Velasco, F., Tornos, F., Daviero-Gomez, V., Gomez, B. & Delclòs, X. 2010. A review of the El Soplao amber outcrop, Early Cretaceous of Cantabria (Spain). *Acta Paleontologica Sinica* 84(4): 959-976.

I.3. **Pérez-de la Fuente, R.**, Nel, A., Peñalver, E. & Delclòs, X. 2010. A new Early Cretaceous snakefly (Raphidioptera: Mesoraphidiidae) from El Soplao amber (Spain). *Annales de la Société entomologique de France* 46(1-2): 108-115.

I.4. Soriano, C., Archer, M., Azar, D., Creaser, P., Delclòs, X., Godthelp, H., Hand, S., Jones, A., Nel, A., Néraudeau, D., Ortega-Blanco, J., **Pérez-de la Fuente, R.**, Perrichot, V., Saupe, E., Solórzano-Kraemer, M. & Tafforeau, P. 2010. Synchrotron X-ray imaging of inclusions in amber. *Comptes Rendus Palevol* 9(6-7): 361-368.

I.5. **Pérez-de la Fuente, R.**, Delclòs, X., Peñalver, E. & Arillo, A. 2011. Biting midges (Diptera: Ceratopogonidae) from the Early Cretaceous El Soplao amber (N Spain). *Cretaceous Research* 32: 750-761.

I.6. **Pérez-de la Fuente, R.**, Peñalver, E., Delclòs, X. & Engel, M. S. 2012a. Snakefly diversity in Early Cretaceous amber from Spain (Neuropterida, Raphidioptera). *Zookeys* 204: 1-40.

I.7. **Pérez-de la Fuente, R.**, Perrichot, V., Ortega-Blanco, J., Delclòs, X. & Engel, M. S. 2012b. Description of the male of *Megalava truncata* Perrichot, 2009 (Hymenoptera: Megalyridae) in Early Cretaceous Spanish amber from El Soplao. *Zootaxa* 3274: 29-35.

I.8. **Pérez-de la Fuente, R.**, Peñalver, E. & Ortega-Blanco, J. 2012c. A new species of the diverse Cretaceous genus *Cretevania* Rasnitsyn, 1975 (Hymenoptera: Evaniidae) from Spanish amber. *Zootaxa* 3514: 70-78.

I.9. Saupe, E. E., **Pérez-de la Fuente, R.**, Selden, P. A., Delclòs, X., Tafforeau, P. & Soriano, C. 2012. New *Orchestina* Simon, 1882 (Araneae: Oonopidae) from Cretaceous ambers of Spain and France: first spiders described using phase-contrast X-ray synchrotron microtomography. *Palaeontology* 55(1): 127-143.

I.10. **Pérez-de la Fuente, R.**, Saupe, E. E. & Selden, P. A. 2012d, *en prensa*. New lagonomegopid spiders (Araneae: †Lagonomegopidae) from Early Cretaceous Spanish amber. *Journal of Systematic Palaeontology*.

I.11. **Pérez-de la Fuente, R.**, Delclòs, X., Peñalver, E., Speranza, M., Wierzchos, J., Ascaso, C. & Engel, M. S. 2012e, *reenviado a la revista tras informe favorable de revisores*. Early evolution and ecology of camouflage in insects. *Proceedings of the National Academy of Sciences USA.*

Anexo I.1

Unusual concentration of Early Albian arthropod-bearing amber in the Basque-Cantabrian Basin (El Soplao, Cantabria, Northern Spain): palaeoenvironmental and palaeobiological implications

Concentración inusual de ámbar del Albiense Inferior con contenido en artrópodos en la Cuenca Vasco-Cantábrica (El Soplao, Cantabria, Norte de España): implicaciones paleoambientales y paleobiológicas.

Referencia completa:

Najarro, M., Peñalver, E., Rosales, I., **Pérez-de la Fuente, R.**, Daviero-Gomez, V., Gomez, B. & Delclòs, X. 2009. Unusual concentration of Early Albian arthropod bearing amber in the Basque-Cantabrian Basin (El Soplao, Cantabria, Northern Spain): Palaeoenvironmental and palaeobiological implications. *Geologica Acta* 7(3): 363-387.

Resumen:

El yacimiento de ámbar de El Soplao, de edad Albiense Inferior, ha sido recientemente descubierto en la Cuenca Vasco-Cantábrica (Norte de España) y ha brindado numerosas piezas de ámbar con abundantes bioinclusiones. El depósito de ámbar se encuentra en una unidad siliciclástica no marina a transicional marina (Formación Las Peñosas) que se incluye en una secuencia marina regresiva-transgresiva, dominada por carbonatos, de edad Aptiense Inferior a Albiense Superior. La Formación Las Peñosas corresponde al episodio regresivo de esta secuencia, y a su vez se divide en dos ciclos regresivos-transgresivos menores. Los depósitos de ámbar asociados a carbón se formaron en ambientes estuarino-deltaicos desarrollados durante el episodio de máxima regresión del más breve de estos ciclos regresivos-transgresivos. El ámbar de El Soplao muestra espectros de Espectroscopía Infraroja Transformada de Fourier similares a otros ámbares del Cretácico de España, y se caracteriza por la abundancia de piezas con forma de estalactita de origen subaéreo. Son abundantes las cutículas de plantas bien preservadas asignadas a los géneros de conífera *Frenelopsis* y *Mirovia* en los niveles donde el ámbar aflora. También aparecen ocasionalmente hojas de los géneros de ginkgoal *Nehvizdya* y *Pseudotorellia*. Las bioinclusiones principalmente corresponden a insectos fósiles de los órdenes Blattaria, Hemiptera, Thysanoptera, Raphidioptera, Neuroptera, Coleoptera, Hymenoptera y Diptera, aunque se han observado algunas arañas y telarañas. Algunos insectos pertenecen a grupos escasos en el registro fósil, como el nuevo morfotipo de avispa *Archaeromma* (de la familia Mymarommatidae) y el ceratopogónido *Lebanoculicoides* (de la subfamilia monogenérica Lebanoculicoidinae). Este nuevo yacimiento de ámbar constituye un hallazgo muy significativo que contribuirá a mejorar el conocimiento y comprensión de la paleofauna no-marina artropodiana.

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Unusual concentration of Early Albian arthropod-bearing amber in the Basque-Cantabrian Basin (El Soplao, Cantabria, Northern Spain): Palaeoenvironmental and palaeobiological implications

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ABSTRACT

The El Soplao site is a recently-discovered Early Albian locality of the Basque-Cantabrian Basin (northern Spain) that has yielded a number of amber pieces with abundant bioinclusions. The amber-bearing deposit occurs in a non-marine to transitional marine siliciclastic unit (Las Peñosas Formation) that is interleaved within a regressive-transgressive, carbonate-dominated Lower Aptian-Upper Albian marine sequence. The Las Peñosas Formation corresponds to the regressive stage of this sequence and in its turn it splits into two smaller regressive-transgressive cycles. The coal and amber-bearing deposits occur in deltaic-estuarine environments developed during the maximum regressive episodes of these smaller regressive-transgressive cycles. The El Soplao amber shows Fourier Transform Infrared Spectroscopy spectra similar to other Spanish Cretaceous ambers and it is characterized by the profusion of sub-aerial, stalactite-like flows. Well-preserved plant cuticles assigned to the conifer genera *Frenelopsis* and *Mirovia* are abundant in the beds associated with amber. Leaves of the ginkgoalean genera *Nehvizdya* and *Pseudotorellia* also occur occasionally. Bioinclusions mainly consist of fossil insects of the orders Blattaria, Hemiptera, Thysanoptera, Raphidioptera, Neuroptera, Coleoptera, Hymenoptera and Diptera, although some spiders and spider webs have been observed as well. Some insects belong to groups scarce in the fossil record, such as a new morphotype of the wasp *Archaeromma* (of the family Mymarommatidae) and the biting midge *Lebanoculicoides* (of the monogeneric subfamily Lebanoculicoidinae). This new amber locality constitutes a very significant finding that will contribute to improving the knowledge and comprehension of the Albian non-marine paleoarthropod fauna.

KEYWORDS | **Arthropod bioinclusions. Fossil resin. Plant cuticles. Lower Albian. Spain.**

INTRODUCTION

Oldest ambers with micro-bioinclusions are known from the Triassic of Italy (Schmidt et al., 2006), but it is not until the Barremian-Aptian of Lebanon that macro-bioinclusions occur more profusely (Azar, 2000; Poinar and Milki, 2001). During the Early Cretaceous, amber-bearing deposits become especially common in the geological record. This was promoted possibly by the rise and spread of conifers, such as the Araucariaceae and Cheirolepidiaceae, and by a palaeoclimate warmer than today due to higher pCO_2 levels and significantly different oceanic circulation and geography (Crowley and North, 1991; Huber et al., 1995; Haywood et al., 2004). Coinciding with the initiation of the moist megathermal zone in the Northern Hemisphere, amber deposits developed between 29ºN-50ºN during the earliest Cretaceous and extended to 27ºN to near 70ºN during the Mid Cretaceous (Morley, 2000). During these periods the Iberian Peninsula was situated at low latitude, along the boundary between wet and warm tropical-"paratropical" climates where coal and other organic-rich rocks were deposited.

Early Cretaceous ambers bearing fossil inclusions are scarce, and such localities are of great scientific interest (Fig. 1). In Cantabria (northern Spain), amber is relatively widespread in the Cretaceous deposits, and has been found previously in minor amounts at least at 23 localities. However, in the past none of these localities had provided amber with arthropod inclusions. An intensive geological survey in the Lower Cretaceous succession of northwest Cantabria recently resulted in the discovery of a new amber locality near Rábago village, within the El Soplao territory (Fig. 1B). This site shows a remarkable accumulation of amber with abundant biological inclusions. The El Soplao amber site occurs within a Lower Albian siliciclastic unit (Las Peñosas Formation [Fm.]; García-Mondéjar and Pujalte, 1982). Preliminary data for this new amber accumulation indicate that this is probably the largest site of amber with arthropod bioinclusions that has ever been found in Spain so far.

This paper deals with i) documenting this new finding of arthropod bearing amber as an unusual concentration, as well as describing its related deposits in terms of major stratigraphic and sedimentological characteristics, description of the associated plant cuticles and bioinclusions, and preliminary study of the amber geochemistry; ii) discussing geological and depositional features that may help in understanding the palaeoenvironmental implications of these deposits and their palaeogeographic context; and iii) providing an appropriate introduction for future, more specific studies, on this exceptional new amber site.

Emphasis is given in providing a solid sedimentological, palaeoenvironmental and palaeogeographic framework of this palaeontologically significant deposit for its exceptional preservation and age.

METHODOLOGY AND TECHNIQUES

Sedimentological and palaeoenvironmental interpretations are based on field observations. Four laterally correlative stratigraphic sections (Puente Arrudo, Rábago, La Florida and Plaza del Monte), belonging to the Las Peñosas Fm., have been logged at a meter-centimetre scale. From these data a W-E cross-section has been established to display the principal depositional and palaeoenvironmental features and the stratigraphic distribution of the amber and coal-bearing unit. Whenever possible, rock sampling and measurement of palaeocurrent orientations of selected structures were carried out to help in sedimentological interpretations.

Pieces of amber were acquired by surface collection during field work in the area. To characterize the El Soplao amber, three Fourier Transform Infrared Spectroscopy (FTIR) spectra of three separate amber samples and one sample of recent kauri resin -*Agathis australis* (D. Don) Lindl. in Loud., 1829- were obtained using an infrared Fourier Bomem DA3 spectrometer, in the Molecular Spectrometry Unit of the University of Barcelona (SCT-UB).

Palaeobotanical samples from plant cuticle-rich claystones were obtained by macerating the clayey sediment in hydrogen peroxide and air-drying the organic residues. Resulting fossil plant fragments were sorted using both the naked eye and the stereomicroscope.

The amber was kept wet during screening in order to improve visibility and to detect arthropod bioinclusions. Screening was done under a stereoscope, using transmitted and obliquely reflected light. The amber pieces were cut around the detected arthropods and then polished to permit optimal study. Drawings of some specimens were made with the aid of an image drawing tube, an Olympus V-DA mounted on an Olympus BX51 stereoscopic microscope. Photomicrographs were made with a digital camera mounted on the same microscope. The specimens are housed provisionally in the "Museo Geominero of the Instituto Geológico y Minero de España" (IGME), in Madrid, Spain.

PALEOGEOGRAPHICAL DISTRIBUTION OF EARLY-MID CRETACEOUS AMBER

Early-Mid Cretaceous (Aptian to Cenomanian) amber occurrences have great scientific interest owing to their scarcity (Fig. 1). In fact, macrobioinclusion-bearing ambers of this age are basically restricted to four Eurasian areas: Northern Siberia (Taimyr Peninsula), southeastern Asia (Myanmar), western Middle-East (Lebanon and Jordan), and southwestern Europe (Spain and France). A review of amber localities in the literature was compiled by Martínez-Delclòs et al. (2004). The four areas were located within the warm temperate and tropical-paratropical palaeoclimatic regions (Fig. 1) *sensu* Scotese (2000), also referred to as tropical and south-subtropical Cretaceous climate belts by Spicer et al. (1994).

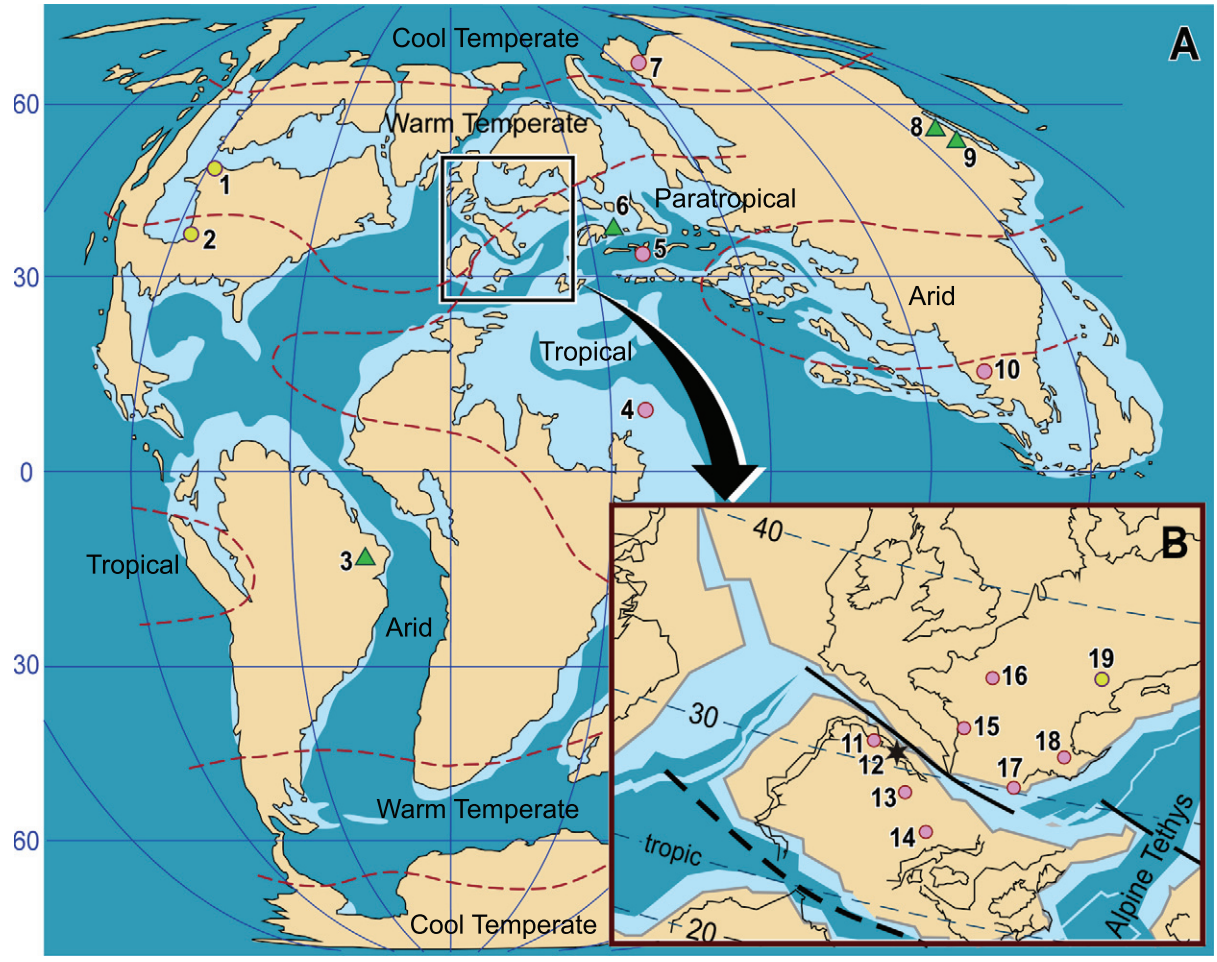

FIGURE 1 | **A) Major Early-Mid Cretaceous (Aptian to Cenomanian) amber occurrences (Redrawn from Blakey, 2008). Amber localities with bioinclusions are symbolized with circles, otherwise green triangles are used. Moreover, yellow circles represent ambers that have only provided microbioinclusions (bacteria, protists, algae and/or fungi). Pink circles account for macrobioinclusion-bearing ambers (essentially arthropods), with the exception of El Soplao amber, which is designated out with a black star. Broken purple lines delimit palaeoclimatic regions *sensu* Scotese (2000). (1) Ruby Creek (Alberta, Canada; Medioli et al., 1990). (2) Ellsworth (Kansas, USA; Waggoner, 1996). (3) Nova Olinda-Santana (Ceará, Brazil; Martill et al., 2005). (4) Middle-East. Wadi Zerka (Amman, Jordan; Bandel et al., 1997; Kaddumi, 2005). Bcharreh, Hammana, and Jezzine, among others (Lebanon; Azar, 2000; Veltz, 2008). Mt. Hermon (North District, Israel; Greenblatt et al., 1999). (5) Yukhary Agdzhakend (Goranboy, Azerbaijan; Ratnitsyn and Quicke, 2002). Russia (Zherikhin and Eskov, 1999; Ratnitsyn and Quicke, 2002). (6) Stary Oskol (Belgorod). (7) Taimyr Peninsula (Northern Siberia). Baikura-Neru Bay in Lake Taimyr (Central Taimyr). Nizhnyaya Agapa River (West Taimyr). Begichev Fm. in the Khatanga River (Eastern Taimyr). (8) Khetana River in South of Okhotsk (Khabarovsk Krai). (9) Suyfun Coal Basin (Primorye). (10) Hukawng Valley (Kachin, Myanmar; Cruickshank and Ko, 2003). B) Amplified area squared at subfigure A, corresponding to SW Europe. Spain (Arbizu et al., 1999; Alonso et al., 2000; Peñalver et al., 2007b; Delclòs et al., 2007). (11) El Caleyu and Pola de Siero (Asturias). (12) El Soplao Territory, near Rábago village (Cantabria, in this paper). (13) Moraza and Peñacerrada-Montoria (Burgos and Álava respectively). (14) San Just (Teruel). France (Nel et al., 2004; Perrichot, 2004, 2005; Néraudeau et al., 2005; Perrichot et al., 2007; Néraudeau et al., 2008; Girard, 2008). (15) Archingeay-Les Nouillers, La Buzinie, Cadeuil, Fouras, l'Ile d'Aix, and Les Renardières (Les Charentes). (16) Ecommoy and Durtal (Sarthe and Maine-et-Loire respectively). (17) Fourtou (L'Aude). (18) Salignac and Sisteron (Alpes-de-Haute-Provence). (19) Schliersee (Bavaria, Germany; Schmidt et al., 2001).**

In Spain, aside from the frequent occurrence of amber in Aptian to Cenomanian deposits, only a few localities show sufficient quantity to be identified as accumulations (Fig. 1B). In the past, only two of these deposits had yielded important amounts of bioinclusions in terms of quantity and quality, specifically the Álava deposits of Peñacerrada and Montoria (Alonso et al., 2000; Delclòs et al., 2007) and the San Just outcrop in Teruel (Delclòs et al., 2007; Peñalver et al., 2007b). In Asturias, although less significant, amber with bioinclusions has been described in El Caleyu and Pola de Siero (Arbizu et al., 1999) (Fig. 1). The identification of the new amber deposit of the El Soplao in Cantabria (Figs. 1 and 2) enlarges the still patchy record of these palaeontological deposits of exceptional preservation in Spain.

GEOLOGICAL AND PALAEOGEOGRAPHIC SETTING

The recently discovered amber outcrop is located in the El Soplao territory in northwestern Cantabria (Fig. 2).

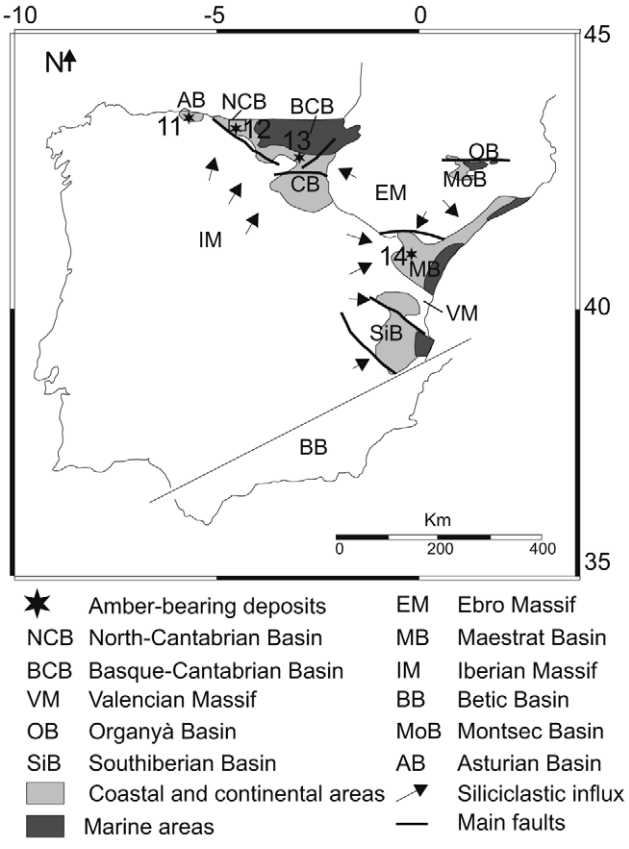

FIGURE 2 | **Map of the Iberian Peninsula showing the location of the Lower Albian basins and the distribution of the Lower Cretaceous amber-bearing deposits (same nomenclature as in Figure 1). (11) El Caleyu and Pola de Siero deposits. (12) The El Soplao deposit. (13) Peñacerrada-Montoria deposits. (14) San Just deposit. (Modified from Salas et al., 2001).**

This area, located immediately to the north of the Cabuérniga Ridge, constituted the northwestern margin of the Basque-Cantabrian Basin during the Cretaceous (Fig. 3). The evolution and current structure of the Basque-Cantabrian Basin are related to the kinematics between the European and Iberian plates (Malod and Mauffret, 1990; Olivet, 1996). The inception of the basin occurred during a Permo-Triassic rifting event. A second extensional phase was related to the opening of the Bay of Biscay during the Late Jurassic-Early Cretaceous (e.g., Rat, 1988; García-Mondéjar et al., 1996). Renewed extension and perhaps strike-slip faulting along a NW-SE trend occurred during the Aptian-Albian (e.g., García-Mondéjar et al., 1996; Martín-Chivelet et al., 2002; Soto et al., 2007). These tectonic events resulted in the development of several extensional sub-basins bounded by synsedimentary faults, in which great thicknesses of sediments accumulated. These sedimentary sub-basins underwent widespread contraction during the Pyrenean Orogeny in Late Eocene-Oligocene times (Hines, 1985; Fernández Viejo and Gallastegui, 2005). Consequently, the present structure of the study area is the result of the inversion of the previous Mesozoic extensional and strike-slip structures.

The studied succession was deposited in the North Cantabrian sub-basin (NCB) (Fig. 3A), which subsided moderately for most of Cretaceous time (Martín-Chivelet et al., 2002; Wilmsen, 2005). The Cabuérgina Ridge (Fig. 3) is an E-W trending fault zone, which bounds this sub-basin to the south. This palaeo-high represents a previous Variscan structure that was reactivated through extensional faulting during the Mesozoic (Rat, 1988; García-Espina, 1997).

Structurally, the studied succession was deposited during the Cretaceous on an eastward tilted block (Fig. 3B). The tilted block forms the footwall of the N-S Bustriguado Fault (BF, Figs. 3A and 3C) that bounds to the west the main Cretaceous depocenter (Figs. 3A and 3B). Recent geological mapping has shown that the BF branches at a corner point with the E-W trending North Cabuérniga Fault (NCF; Fig. 3A); (García-Senz "pers. comm."), forming an extensional-linked system, as in the examples described by Gibbs (1990). Because in the northern margin of the Iberian plate, the direction of extension during the Cretaceous is considered to be roughly orthogonal to the Cantabrian margin (Malod and Mauffret, 1990), the BF is interpreted as a left-lateral transfer fault, and the NCF as the corresponding frontal extensional ramp. The tilted block that contains the El Soplao territory dips and thickens towards the master BF (Fig. 3B), a feature commonly interpreted as the result of extensional fault propagation folding (Withjack et al., 1993). Models of such faults have been described in

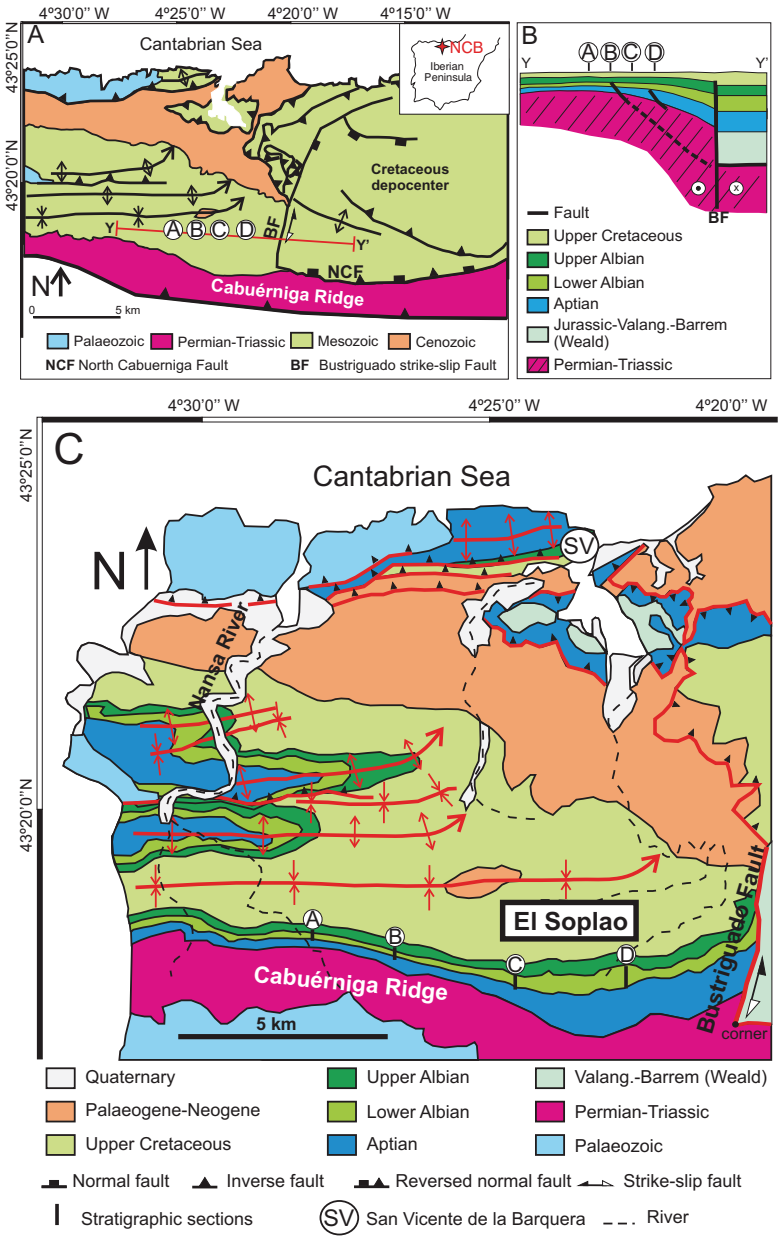

FIGURE 3 | **A) Geological sketch with the main structural elements of the North Cantabrian sub-basin (NCB). The red line Y-Y' indicates the position of the cross-section of Fig. 3B. B) Schematic cross-section showing the restored geometry of the NCB in the El Soplao territory during the Cretaceous. Figure not to scale. C) Detailed geological map of the NCB Basin in the El Soplao area with location of the stratigraphic sections studied. (A) Puente Arrudo Section, (B) Rábago Section, (C) La Florida Section, (D) Plaza del Monte Section.**

frontal ramps (Withjack et al., 1993) but few examples in transfer faults are known. This Cretaceous configuration was inverted during the Palaeogene folding and the faults reversed their movement. The NCF behaved as a frontal thrust ramp, and the BF as a right-lateral strike-slip fault. The latter passes northwards to an oblique thrust sheet that superposes the Cretaceous on the Cenozoic.

STRATIGRAPHY OF THE EL SOPLAO AREA

The bulk of the Mesozoic succession of the El Soplao area lies unconformably on folded (Variscan deformation) Carboniferous basement (Fig. 4). This succession was initiated with a thick sequence of Lower Triassic continental red sandstones and mudstones (Buntsandstein facies). Late Triassic, Jurassic and earliest Cretaceous sequences are absent in the studied area, probably because during the Late Jurassic-Early Cretaceous rifting stage, the area to the north of the Cabuérniga Ridge was subjected to erosion and nondeposition. Subsidence renewed in the Early Aptian and was accompanied by gradual marine transgression. Thus, the Aptian-Albian succession of the El Soplao area, unconformably overlies Triassic strata and was dominated by shallow marine carbonate deposition (Fig. 4).

As a whole, the Aptian-Albian succession of the El Soplao territory constitutes an E-W elongated lithosome

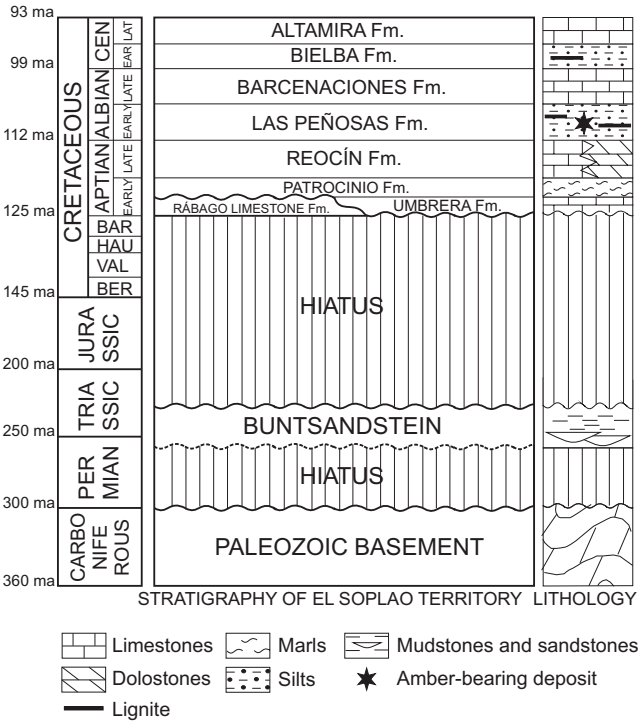

FIGURE 4 | **Carboniferous to Upper Cretaceous lithostratigraphy of the El Soplao area (modified from Hines, 1985). Chronostratigraphy after Gradstein (2004).**

9 km long with wedge-shaped geometry deepening and thickening eastward, on the slope of the tilted block active during this time (Najarro et al., 2007) (Fig. 3B). Thicknesses vary from about 600 m in the eastern part of the tilted block (Bustriguado area, Fig. 3) to less than 200 m toward the west (Puente Arrudo-Rábago Sections, Fig. 3C). The general stratigraphic and biostratigraphic framework of the Aptian-Albian lithological units has been established by Ramírez del Pozo (1972) and Hines (1985), but the main depositional systems and sequences have been revised recently (Najarro et al., 2007; Najarro and Rosales, 2008). A simplified stratigraphy of this interval is provided, adapted from the terminology by Hines (1985) for the major lithological units (Fig. 4).

The Early Aptian marine transgression led to deposition of shallow platform carbonates of the Lower Aptian Rábago Limestone Fm. and Umbrera Fm. that spread over the studied area. Continued transgression during the Early Aptian caused platform drowning, and resulted in deposition of relatively deep-water marls (Patrocinio Fm.) that covered the entire carbonate platform (Najarro and Rosales, 2008). Subsequent gradual regression led to deposition of shallow water carbonates of the Reocín Fm. during the Late Aptian, and finally delta-estuarine siliciclastics and carbonaceous lutites of the Las Peñosas Fm. during the Early Albian (Fig. 4). The vertical evolution from the Upper Aptian Reocín Fm. to the Lower Albian Las Peñosas Fm. is interpreted herein as a relative sea-level fall associated with a deltaic progradation. The Upper Albian succession follows with deposition of the Barcenaciones Fm. (Fig. 4), a shallow water carbonate bank that expands more than 50 km throughout the North Cantabrian sub-basin, as a result of a transgression following deposition of the Las Peñosas Fm. A subsequent regression during the Lower Cenomanian deposited the transitional marine siliciclastic Bielba Fm. Later, deeper water conditions were established during the Late Cretaceous, leading to deposition of open-platform carbonates for the remainder of the Cretaceous succession.

LAS PEÑOSAS FORMATION

Primarily, this paper examines the Lower Albian heterolithic amber-bearing deposit that is included within the Las Peñosas Fm. Regional palaeogeographical and palaeoenvironmental reconstructions of the Basque-Cantabrian Basin during this time slice (García-Mondéjar, 1990) indicate that siliciclastic sediment was transported from highlands and continental areas located to the west and south towards the north during deposition of the Las Peñosas Fm. This amber-bearing unit is approximately equivalent in age and facies to the broadly extended Escucha Fm., deposited to the south of the Basque-Cantabrian Basin (Barrón et al., 2001; Martínez-Torres et al., 2003), as well as other Mesozoic basins of northeastern Spain, including the Maestrat Basin (e.g., Salas and Martín-Closas, 1991; Salas et al., 1991; Querol et al., 1992; Salas et al., 2001; Rodríguez-López and Meléndez, 2004; Rodríguez-López et al., 2005, 2007; Peyrot et al., 2007; Moreno-Bedmar et al., 2008). These units basically represent littoral facies dominated by delta-estuarine deposits, which can be laterally correlated in a NW-SE direction for more than 500 km, from northeastern Cantabria, through the southeast Basque-Cantabrian Basin in the Álava region (Basque Country), and into the Maestrat Basin in Teruel to the Alicante Province (Fig. 2). These areas, which trace the approximate location of the coastline during the Early Albian, are characterized by the presence of coal-bearing deposits with common presence of amber (Delclòs et al., 2007).

Facies and sequence arrangement

The Las Peñosas Fm. previously has been described as a unit formed by a complex of fluvio-estuarine channel sandstones, overbank black carbonaceous mudstones, tidal channel bars and tidal flat facies, and minor intercalations of carbonate beds, exhibiting unclear internal organization (García-Mondéjar and Pujalte, 1982; Hines, 1985). However, detailed stratigraphic and sedimentologi-

cal logging of four W-E correlative stratigraphic sections (the Puente Arrudo, Rábago, La Florida and Plaza del Monte sections; Fig. 3) in the El Soplao region has revealed the depositional architecture of the Las Peñosas Fm. and the stratigraphic distribution of the coal- and amber-bearing deposits (Fig. 5). A summary of the general facies associations, depositional environments and their sequential arrangement is given in this section and summarized in Fig. 5 and Table 1.

It is significant that the facies distribution within the Las Peñosas Fm. displays a clear tectonic control, as suggested in the study area by the strong lateral thickness variation in an E-W direction (Fig. 5), which, in the studied area, ranges from between 45 m to the west to more than 100 m to the east. In this way, the Rábago Section that contains the amber deposit represents the highest point of the flexured footwall block of the Bustriguado fault (Fig. 3B) at the time of deposition of the Las Peñosas Fm. This flexure seems to be accommodated by several minor synsedimentary faults that delineate the structure observed in the Rábago Section (Figs. 3B and 5).

The Las Peñosas Fm. can be informally split into three correlatable units, which are named in this paper, from base to top, Las Peñosas 1 to 3 (P1-P3; Figs. 5 and 6A).

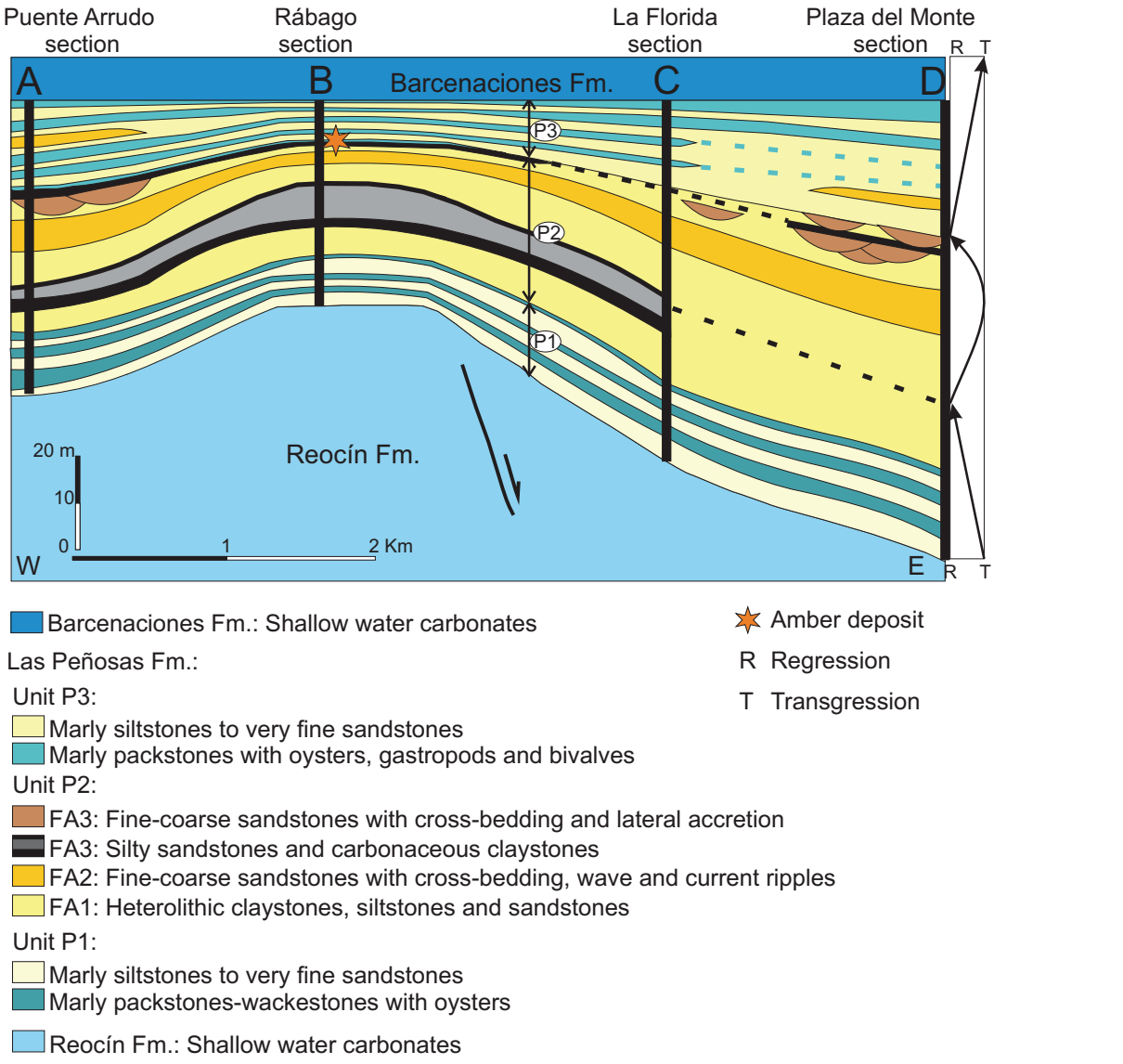

FIGURE 5 | **Stratigraphic correlation of the four studied sections (A to D in Figure 3). Note the location of the amber deposit and the thickness variation of the Las Peñosas Fm. along the W-E cross section (see also Fig. 3). (P1-P3) Members of the Las Peñosas Fm. (see text for explanation). (FA1-FA3) Sedimentary facies associations studied in the Las Peñosas Fm. Amber accumulation usually occurs at the P2-P3 unit boundary.**

TABLE 1 | **Characteristics of the facies associations in the Las Peñosas Fm.**

Unit	FA	F	Lithology	Primary Structures	Vertical Stacking	Interpretation
P3			Alternation of nodular marly-packestones with bioclasts and heterolithic levels of mud- silt- and fine to medium grain-sized sandstones	Wavy, flaser and lenticular lamination	Progressive upward increase in carbonate content	Carbonate-siliciclastic mixed platform
P2	FA3	F6	Weakly cemented, moderate-well sorted, very fine- coarse to grained sandstones in erosionally-based, channalized units. Accretion surfaces with silty clay, plant remains, coal and mudclasts. Iron cemented ripples, pyritized trunk fragments and pyritized burrows at the top.	Large scale trough-, longitudinal-, low angle- and small-ripple-cross bedding; lateral accretion; horizontal-and sigmoidal-stratification; complex deformations	Fining upward	Delta plain: Distributary meandering channels
		F5	Dark organic, sulphide-rich mudstones with bivalves, gastropods, leaves, coal, trunks, sulphide nodules and amber	Wavy and lenticular lamination; current ripples	Rhythmic alternations	Delta plain: Interdistributary bay
		F4	Silty very fine sandstones with coal layers, sulphide nodules, trunks and amber		Rhythmic alternations	Delta plain: Interdistributary bay
	FA2	F3	Weakly cemented, moderated to well-sorted fine to coarse-grained sandstones with mud drapes and mudclasts	Large scale trough cross-bedding; planar cross-bedding; wave ripples	Coarsening and thickening upwards	Delta front: Distributary mouth-bars
	FA1	F2	Sulphide mudstone-siltstones with coal and trunk fragments. Minor to moderate bioturbation	Wavy and lenticular lamination	Fining upward	Wave- and tidal influenced estuarine-delta bay
		F1	Pale-yellow, very fine- to medium-grained, well-sorted sandstones. Mudclasts and coal fragments. Minor to abundant bioturbation dominated by *Skolithos* and track traces.	Low angle and horizontal lamination; planar cross-stratification; flaser and wavy lamination; wave and current-ripples		
P1			Alternation of bioclastic, oyster-rich limestones and bioturbated, nodular marly–silty limestones to siltstones with very fine sand levels	Wavy lamination	Upward decrease in carbonate content and progressive increase in siliciclastics	Transition from shallow carbonate platform to estuarine-delta bay

FA: Facies association. F: Facies

The lower Unit P1 overlies the Reocín Fm. It ranges from about 11 m (Rábago Section) to 40 m (Plaza del Monte Section) and it is characterized by an alternation of bioclastic, oyster-rich limestones and bioturbated, nodular marly-silty limestones to siltstones with intervals of very fine sands. The overall succession presents an upward decrease of carbonate content and a progressive increase in the quartz silt and sand content of the marly intervals. This succession is interpreted as a transitional unit from a shallow carbonate platform to a siliciclastic estuary-delta bay, caused by rapid change in the sedimentary conditions resulting from deltaic progradation.

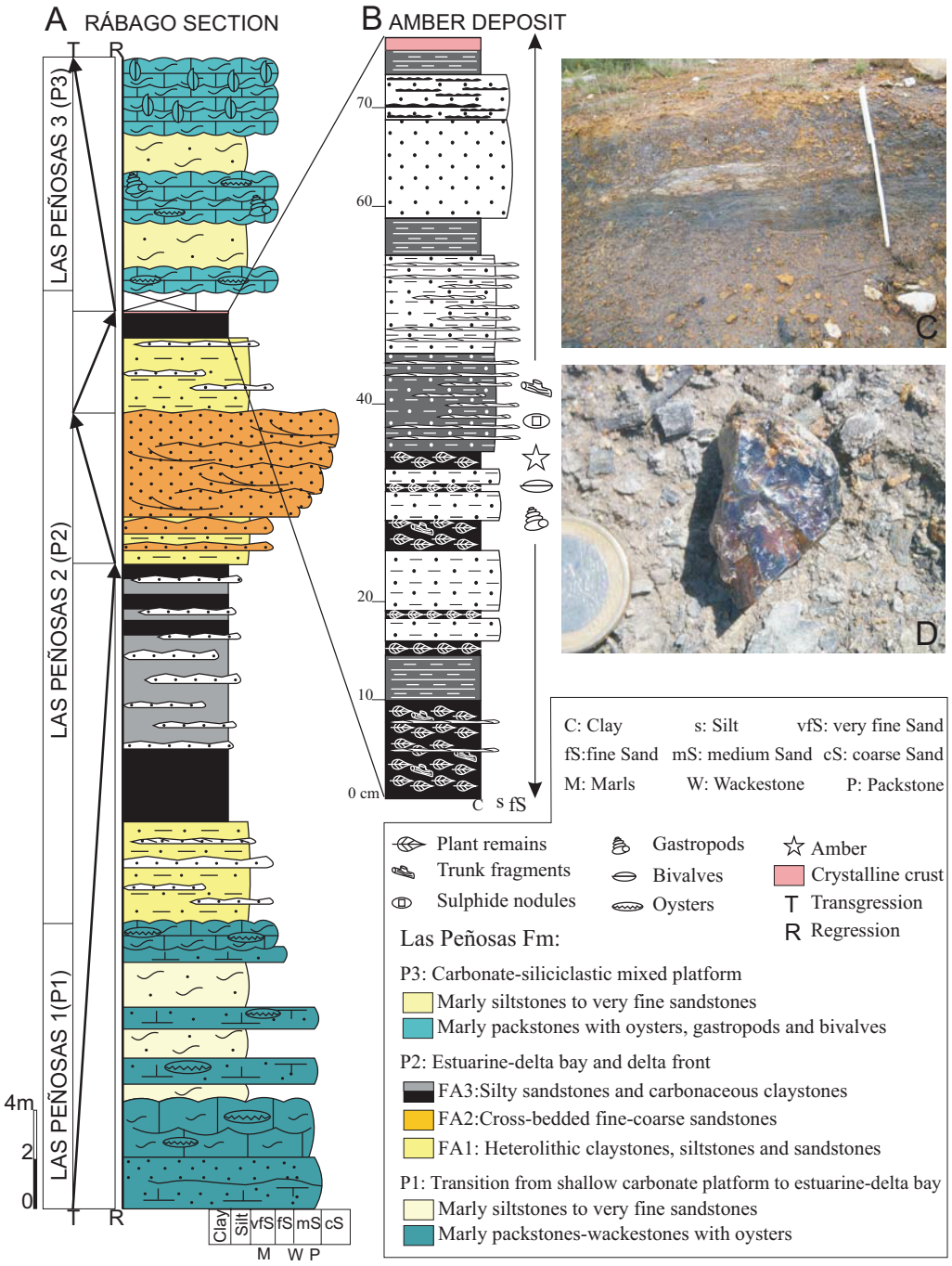

FIGURE 6 | **A) Simplified stratigraphic log of the Rábago Section. Two regressive-transgressive cycles are defined. Note that the position of the amber deposit coincides with the maximum regression of the second cycle. B) High-resolution stratigraphy of the amber deposit. C) General view of the amber deposit (scale: 1m). D) Example of a blue amber piece in situ.**

The middle Unit P2 contains the amber-rich deposit that has been recently discovered in the Rábago Section (Figs. 6B-D and 7A). It lies on top of P1 and ranges in thickness from 25 m (Rábago Section) to 60 m (Plaza del Monte Section; Fig. 5). This unit consists predominantly of heterolithic sandstones-siltstones and carbonaceous mudstones deposited in broadly coastal estuarine and delta environments. Facies associations can be grouped into three main depositional environments. First is delta front facies association without evidence of emergence, interpreted largely as shallow marine. This environment includes distributary mouth-bar facies, deposited mostly, if not entirely, under marine conditions, as well as distal bar, nearshore to offshore deposits. Second are wave- and tide-influenced estuarine-delta bay deposits. Third is delta plain facies association, with sedimentary facies that reflect deposition in both distributary meandering channels (Fig. 7B and Table 1) and infilling of interdistributary bays (Figs. 6C and 7C), the latter with high accumulation of coal, plant cuticles (Fig. 7D) and amber pieces

FIGURE 7 | **Field pictures of the Las Peñosas Fm. A) General view of the new discovered amber-rich deposit in Rábago Section within the Unit P2. B) FA3: Distributary meandering channel with trough cross-bedding, sigmoidal and horizontal stratification and lateral accretion within the Unit P2 in La Florida Section. C) FA3: Interdistributary bay facies within the Unit P2, capped by an erosive transgressive surface (ravinement), and overlain by marine limestones (Unit P3) (Puente Arrudo Section). D) FA3: Exceptionally well-preserved plant cuticle compressions that appear associated with the amber-rich deposit in Rábago Section. E) Detail of FA1 constituted of interbedded mudstones-siltstones with wavy and lenticular lamination and fine-grained sandstones. Unit P2 in Plaza del Monte Section. F) Marly level with high concentration of bivalves at the top of the Unit P3 in Rábago Section.**

(Fig. 6D). Due to the sedimentological and palaeontological importance of this unit, more detailed stratigraphic characteristics and environmental interpretation is provided in the next section.

The Unit P3 superposed the Unit P2 by an erosive transgressive surface (a *ravinement*; Fig. 7C) and in turn is overlain by the Barcenaciones Fm. The thickness of the Unit P3 varies from 13 m to the west (Rábago Section) to 40 m to the east (Plaza del Monte Section; Fig. 5) and is characterized by the stacking of several meter-scale mixed siliciclastic-carbonate sequences. Contrasting with P1, the vertical stacking pattern of P3 presents a progressive increase in the carbonate content toward the top of the unit. This unit is interpreted as a transition from estuarine bay deposits (Fig. 7E) to a shallow carbonate platform system. Thus, a carbonate-siliciclastic mixed platform is proposed. The contact with the overlaying Barcenaciones Fm. is taken at the base of a marly-nodular limestone bed with large bivalves that indicates the definitive abandonment of the siliciclastic system (Fig. 7F).

The amber-rich deposit in the Rábago Section

As noted above, the recently discovered site of amber accumulation is located at the top of Unit P2 in the Rábago Section, where this unit is comprised of three facies associations (Fig. 6 and Table 1).

Facies association 1 (FA 1): wave- and tide-influenced estuarine-delta bay

This facies association consists of heterolithic alternations of thinly bedded dark coloured mudstones, siltstones and sandstones, stacked vertically in meter-scale sequences with a general fining-upward trend. The sequences range in thickness from 3 to 4 m. This facies association displays two sedimentary facies. Facies 1 consists of 5 to 40 cm thick, pale-yellow, very fine- to medium-grained, well-sorted sandstones. The basal contacts are flat and sharp, while the contacts in the top are wavy due to ripples. This facies is characterized by low angle and horizontal lamination, planar cross-stratification, flaser and wavy lamination and wave and current ripples at the tops of the beds. Both current and wave ripples are associated with flaser bedding, and current ripples are seen as climbing in some places. Palaeocurrents have been measured in some crests of the wave ripples resulting in a shoreline direction with an overall E-W trend. Mud drapes occur frequently with thicknesses up to 0.5 cm. Mudclasts and coal fragments appear locally. Bioturbation ranges from sparse to elevated but is consistently characterized by a low diversity assemblage dominated by *Skolithos* and various track traces. Facies 2 consists of beds of mudstone to siltstone. These beds are relatively sulphide-rich and range from 0.5 to 2 m thick, which often combine with facies 1 to form wavy and lenticular bedding (heterolithic facies). Coal and pyritized trunk fragments up to 20 cm long are concentrated at the base of these beds. Minor to moderate bioturbation and sulphide nodules also are present.

The presence of wave and current ripples occurring both as lenticular and flaser bedding, along with the wavy lamination and wave ripples on some sandstone beds, suggests a tidal- and wave-influenced estuarine-delta bay environment (e.g., Reineck and Wunderlich, 1968; Reineck and Singh, 1975; Dalrymple, 1992; Willis, 1997; Kuecher et al., 1990; Folkestad and Satur, 2008). The suite of trace fossils described above may occur in such an environment (Pemberton et al., 1992). The common occurrence of mud drapes and rhythmic bedding of sandstones and mudstones suggests involvement of tidal processes in the formation of this facies (Visser, 1980), but the occurrence of wave-generated structures suggests that reworking also was controlled by waves. The climbing current ripples indicate rapid deposition of sand (Reineck and Singh, 1975). These deposits are interpreted to have originated in the intertidal part of an estuarine-delta bay.

Facies association 2 (FA 2): Delta front distributary mouth-bars

Facies 3 consists of weakly cemented, moderate to well-sorted, fine to coarse-grained sandstone, organized in a coarsening and thickening upwards sequence of about 6 m thick. Sedimentary structures grade vertically from large-scale trough cross-bedding to planar cross-bedding with wave ripples at the top. Mud drapes and mud pebbles are present in foresets. Although preservation at the outcrops prevents detailed sedimentological observations and measurements, in most instances, unidirectional, diffuse palaeocurrent features are observed.

The thickening and coarsening upward trend of this facies association suggests a progradational character. The upward transition from trough cross-bedding to wave ripples at the top suggests decreasing energy conditions. Moreover, the occurrence of mud drapes and mud clasts suggests fluctuating energy conditions likely produced by tidal processes occurring during deposition (Reineck and Singh, 1975; Dalrymple et al., 1990; Shanmugam et al., 2000; Kitazawa, 2007). The presence of wave-ripple lamination also indicates wave influence. As a whole, this facies association is interpreted as a progradation of distributary mouth-bar deposits and sand bars into a wave and tidal influenced estuarine-delta bay.

Facies Association 3 (FA 3): Interdistributary bay

This facies association is composed of a very thin intercalation of silty to very fine sandstones (facies 4) that contain dark organic- and sulphide-rich mudstones (facies 5), ranging in thickness from 0.7 to 2.5 m. Facies 4 is greyish-brown reaching a maximum thickness of 10 cm. It presents wavy and lenticular lamination with current ripples, coal layers (up to 3 cm), sulphide nodules, partially pyritized trunk fragments, minor bioturbation as pyritized burrows, and amber. Facies 5 is mostly composed of layers formed by the accumulation of leaves and other plant remains. These leaves are very well preserved, showing many original details and their venation patterns. When present, the matrix between the plant-bearing levels consists of clay. Also present in this facies are small pyritized moulds of marine gastropods and bivalves, sulphide-nodules (up to 6 cm in size), coal, trunk fragments (up to 15 cm), and abundant pieces of amber. Although amber fragments have been found in all stratigraphic sections, the most abundant yield comes from the Rábago Section, where they consist of both stalactite-shaped and globular or kidney-shaped amber pieces. At the top of this facies association a 5 cm thick crystalline crust appears. The crust surface is colonized by serpulid worm tubes and its genesis remains uncertain. A pale-yellow silty rooting level with associated white mottling occurs in the Plaza del Monte Section at a stratigraphic position laterally equivalent to this crystalline crust.

Dark organic-rich mudstone deposits are interpreted as extensive accumulations of plant remains with a relatively low input of clastic material followed by relatively rapid burial to prevent decomposition (Dalrymple, 1992; Folkestand and Satur, 2008). Mudstones were mostly deposited in interdistributary and coastal bays with a high supply of continental organic matter transported by fluvially associated floods that undoubtedly originated during rainstorm periods. The exceptional preservation of the leaves, along with the presence of pyrite, organic remains, and the low-diversity of fossil traces and benthic fauna, suggest suboxic conditions within the interphase water-sediment. Occasionally, the combined action of spring tides, storms and overbank floods was strong enough to deposit silty and very fine sand layers (Reineck and Singh, 1975; Noe-Nygaard and Surlyk, 1988; Dalrymple, 1992). This inference also is supported by the presence of thin shell remains. The root activity at the top of the infilling sequence implies eventual subaerial conditions, and the development of a horizon exposed to vegetative processes in a palaeosol (McCarthy and Plint, 2003; Folkestand and Satur, 2008). This event is coincident with the maximum regressive stage within the Las Peñosas Fm.

Deposicional sequences and facies model of the amber-bearing deposits

Within the Las Peñosas Fm., amber accumulation occurs principally towards the top of the Unit P2, in dark organic-rich mudstones that deposited in interdistributary bays between meandering distributary channels (i.e., facies association 3; Fig. 8 and Table 1). The vertical stacking of the described facies association of the Unit P2 suggests that it internally displays two smaller transgressive-regressive cycles, with the coal-bearing deposits developing during the regressive phase of the cycles (Fig. 5). These deposits are underlain by shallow marine, siliciclastic and carbonate deposits formed under relatively higher sea-level conditions (Unit P1). The Unit P2 is capped by an erosive transgressive surface (*ravinement*), overlain by full-marine limestones (Fig. 7C). These deposits represent a marked landward shift in the siliciclastic coastal facies, displaying a retrogradational-aggradational stacking pattern (Unit P3). Therefore, deposition of the amber and coal rich levels was coincident with the maximum regressive episode of the estuary-delta progradation (Fig. 5), and represents a relative sea-level fall. The same pattern in coal- and amber-rich deposits has also been described for the Escucha Fm., in the south of the Basque-Cantabrian Basin (Peñacerrada-Montoria outcrops; Martínez- Torres et al., 2003), in the Maestrat Basin (Rodríguez-López et al., 2005), and in the Oliete sub-basin along the San Just outcrop (Peñalver et al., 2007b), both in the Teruel Province. In all these areas amber deposits were related to the progradation of a delta-estuarine system. In Peñacerrada-Montoria, amber accumulated in interdistributary bays within lower delta plain environments (Martínez-Torres et al., 2003), whereas in San Just, amber was deposited in freshwater ponds both within the upper delta plain and in the lower delta plain (Querol et al., 1992). Despite of the similarities between the depositional environments of all the amber-rich deposits of the Lower Cretaceous of Spain, it is worth noting that the depositional environment of the El Soplao amber presents a slight marine influence, as it can be inferred from the presence of some small marine bivalves and gastropods within the amber deposit and bryozoans and serpulids incrusting the surface of some amber samples. In the amber from southwestern France, marine influence has been pointed out as well, but directly evidenced from marine microfossil inclusions like marine diatoms, radiolarians, sponge spicules, and foraminifers (Girard et al., 2008). On the contrary, amber deposits from Lebanon (Azar et al., 2003; Veltz, 2008) and the Isle of Wight (United Kingdom) (Jarzembowski et al., 2008) were accumulated in more proximal delta environments and fluviatile channel deposits with a larger continental influence.

Stratigraphic models for clastic deposition generally suggest that regressive wave-dominated shallow marine systems develop during sea-level falls, whereas tidally

influenced paralic coal-rich deposits develop during the transgressive infilling of incised valleys (e.g., Allen and Posamentier, 1993). The majority of these case studies came from areas with relatively simple tectonic settings and subsidence patterns, such as the Cretaceous of the Western Interior Seaway in North America (Posamentier and Vail, 1988) and Quaternary successions along passive margins (e.g., Allen and Posamentier, 1993). In these studies, the tectonic influence on sequence arrangement is relatively minor and the eustatic fluctuation in sea level is the principal control on stratal succession. In contrast, the Las Peñosas Fm. was deposited in rifting setting during a period of major tectonic rearrangement across the entire Basque-Cantabrian Basin, with active faulting that resulted in uplift and marked subsidence changes over short distances (García-Mondéjar et al., 1996, 2003). It is in this context that local regression occurred with coeval progradation of siliciclastic coastal deposits.

THE AMBER

General characteristics and morphological types

Trees can produce different kind of resins depending on what structural part is noted, such as roots, trunk, branches and leaves (Langenheim, 1995). It has long been known that resins are exuded outside the plant as defence from megaherbivores, insects, and pathogens, such as fungi (especially in the tropics), viruses, other microbes and bacteria. Presently, no methodology is available to differentiate what parts of the tree were involved in the origin of different amber types. Due to the relative abundance of amber at several outcrops, it is generally supposed that the exudation of the original resin occurred mainly in trunks. Our observations of *Agathis australis* in New Zealand subtropical forest suggest that roots were probably significant producers of resin during the past, attributable to copious exudations of root-generated resin.

The new Albian deposit described herein is unusually rich in amber flows of different types formed under aerial conditions by liquid resin (containing flow structure). Normally, these flows are very rich in bioinclusions, especially small insects. The richest flows are stalactite-shaped amber pieces (Figs. 9A-9B). These cylindrical or subcylindrical pieces commonly contain very well preserved bioinclusions in clear yellow amber. The amber flows also include sub-spherical or elongated specimens with a pattern of striations and bulges and apparently an attached scar suggesting a bark pattern. This morphology indicates that the flows

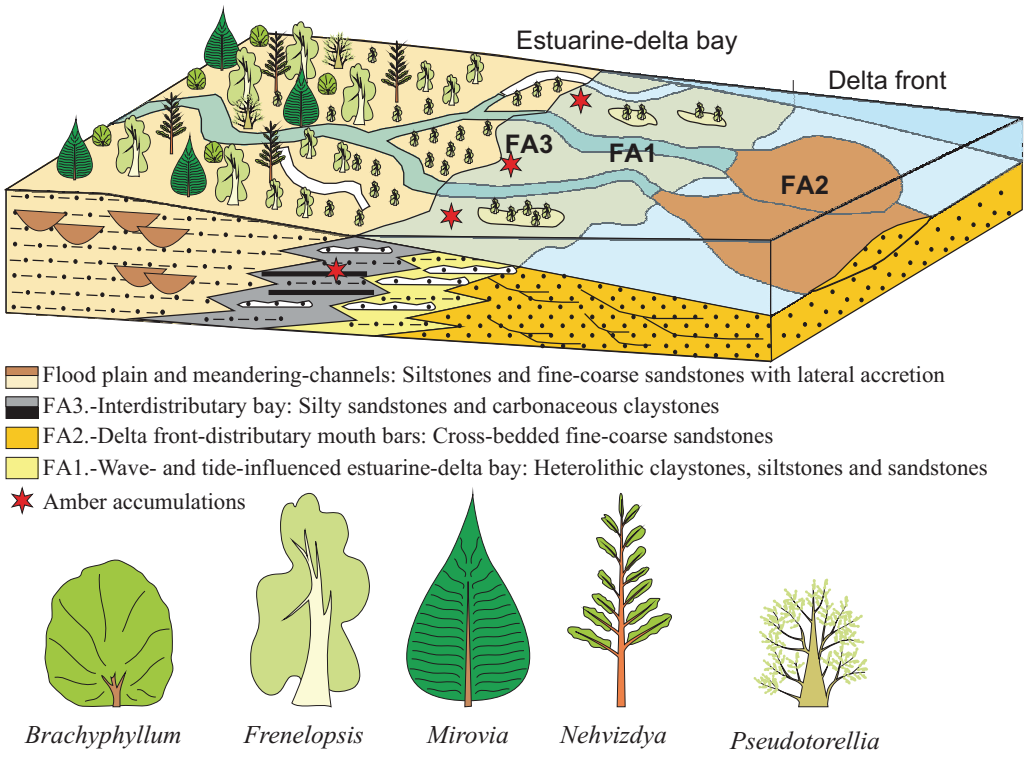

FIGURE 8 | **Block diagram illustrating an idealized model of the depositional environments during sedimentation of the amber- and coal-rich levels. The accumulation of amber- and coal-rich sediments took place during the maximum regressive episode of the estuarine-delta progradation. FA: Facies association.**

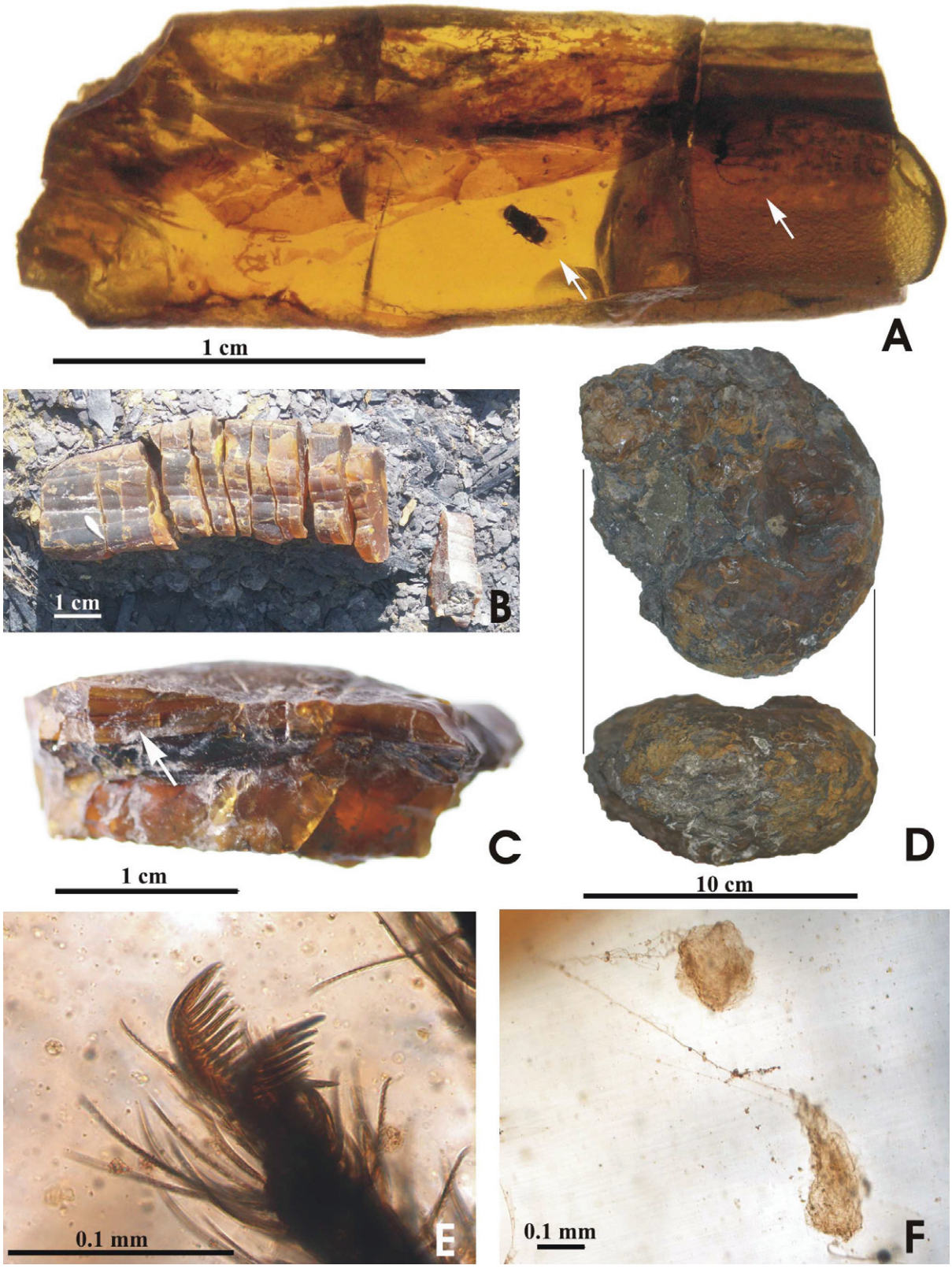

FIGURE 9 | **Different types of amber pieces and amber bioinclusions related to spiders from El Soplao (Rábago, Cantabria). A) Stalactite-shaped amber flow with a wasp of the family Megaspilidae -left arrow- trapped on a spider web fragment (see detail of the spider web in 9F) and two insects shown in figure 12C -right arrow-. B) Stalactite-shaped amber flow exposed in situ which contained a scelionid wasp. C) Amber flow (crust); arrow indicates some flows that originated from liquid resin and cover a copious flow of dark amber. D) Big kidney-shaped mass in two views. E) Pectinate paired claws, adapted to efficient handling of silk and locomotion on an aerial web, present in an Araneoidea spider. F) Detail of the spider web fragment which trapped a megaspilid wasp. Images E and F were made with integrated consecutive pictures taken at successive focal planes.**

originated by viscous resin under aerial conditions. The viscous resin avoided capture of insects and plant debris due to the short time that these structures remained surficially sticky. Other specimens are plain or unelaborated in shape with several layers accumulating by different flows by less viscous resin with marks indicating aerial conditions (Fig. 9C). This last type usually contains abundant bioinclusions.

A different type are the kidney-shaped masses, normally very large in size (up to a decimetre in diameter) with an external surface slightly granulose that lacks evidence of aerial exposure (Fig. 9D). Some authors consider that this type of mass had formed by subterranean resin secretion from roots, probably explaining their lack of bioinclusions. These amber masses also are abundant in the El Soplao outcrop.

Of gemmological interest, abundant blue amber pieces (Fig. 6D) were found, similar to the noted blue amber from the Dominican Republic (Bellani et al., 2005). Both are the only well-known occurrences of this type of amber. A fluorescent blue glow appears in these pieces under normal sunlight, and under ultraviolet light it glows a bright milky-blue. In contrast, under artificial light these fragments show the typical honey-reddish colour of the Cretaceous amber.

Geochemistry

The Fourier Transform Infrared Spectroscopy (FTIR) is a solid-state spectroscopic technique usually used to characterize ambers (Langenheim and Beck, 1965). Nevertheless, the majority of fossil resins of the same geological range often show similar patterns preventing objective classification. Gas Chromatography-Mass Spectrometry (GC-MS) determines the individual non-volatile amber compounds and their molecular structure, and also suggests the plant producer (Grimalt et al., 1988; Chaler and Grimalt, 2005). Previous GC-MS studies on Cretaceous amber from Álava (southern Basque-Cantabrian Basin) indicate that some isolated compounds found may have originated from agathic acid, suggesting that the genus *Agathis*, or a close genus of Araucariaceae (Coniferales), was the amber producer (Alonso et al., 2000; Chaler and Grimalt, 2005). The palynological study supported this indication, because it revealed that a high percentage of pollen grains related to Araucariaceae (Barrón et al., 2001). Nevertheless, currently no araucariacean meso- or macro-remains have been found within the Álava amber or in the surrounding rock.

Here, we compare the FTIR of recent *Agathis australis* resin and amber samples from El Soplao (Fig. 10). The *Agathis* resin is a mixture of mono-, sesqui- and diterpenes, and each of its 13 species has a characteristic mixture of diterpenoid acids. Today this araucariacean genus produces large quantities of resin under natural conditions which polymerize rapidly, forming indurated masses. Recent studies from the Álava amber (Chaler and Grimalt, 2005) indicate that all samples show branched monoalkybenzenes, bicyclic sesquiterpenoids and tricyclic diterpenoids related to pimaric acid precursors, suggesting a distinctive palaeobotanic origin from *Agathis*-like species.

Three amber samples were analysed from the El Soplao amber: i) a fragment of a stalactite-like amber piece from an organic-rich clay level (AMB82); ii) a fragment of large kidney-shaped mass, red in colour, found in an organic-rich sand layer (AMB80), and iii) a fragment of orange kidney-shaped mass from an organic-rich clay level (AMB81). A fragment of stalactite-shaped dry resin from *Agathis australis* also was analysed for comparison (AMB83). The FTIR spectra obtained are shown in Fig. 10.

Structural changes in the organic components of the amber samples are due to maturation processes during rock diagenesis. In the evaluation of the maturity of the coal and organic matter from the Escucha Fm. and other Early Cretaceous Spanish basins, such as the Maestrat Basin and the Basque-Cantabrian Basin, the thermal analysis based on the vitrinite reflectance (%R) suggests around 52ºC as maximum temperature from modelling (Sangüesa and Arostegui, 2003; Permanyer, pers. comm.) The FTIR analyses (transmittance and absorbance) of the amber pieces of El Soplao show that all three spectra are practically identical. The IR spectra of all samples exhibited the same bands, but with different intensities (Fig. 10). In absorbance, all spectra show similar relative intensity, but in the sample AMB80, which corresponds to a red amber fragment, the intensity decreases at wave-numbers 727 and 814 cm^{-1}, and increases considerably at approximately wave-number group 1714 cm^{-1}, a complex band associated with carboxyl groups (Fig. 10). In this sample we also observe broad absorption bands at ca. 3460 and 1635 cm^{-1}, the signal due to water or possibly to weathering. The spectra coincide in the major features with the previous results obtained from other Spanish Cretaceous ambers (see FTIR spectra in Alonso et al., 2000; Chaler and Grimalt, 2005; Peñalver et al., 2007a, 2007b; Corchón et al., 2008). All the spectra are dominated by small C-H stretching bands near 2950 cm^{-1}, C-H banding occurs between 1470 and 1380 cm^{-1}, and the carbonyl bands are close to 1700 cm^{-1}. The lack of exocyclic methylenic bands at 880, 1640 and 3070 cm^{-1} is consistent with the high maturity of the amber.

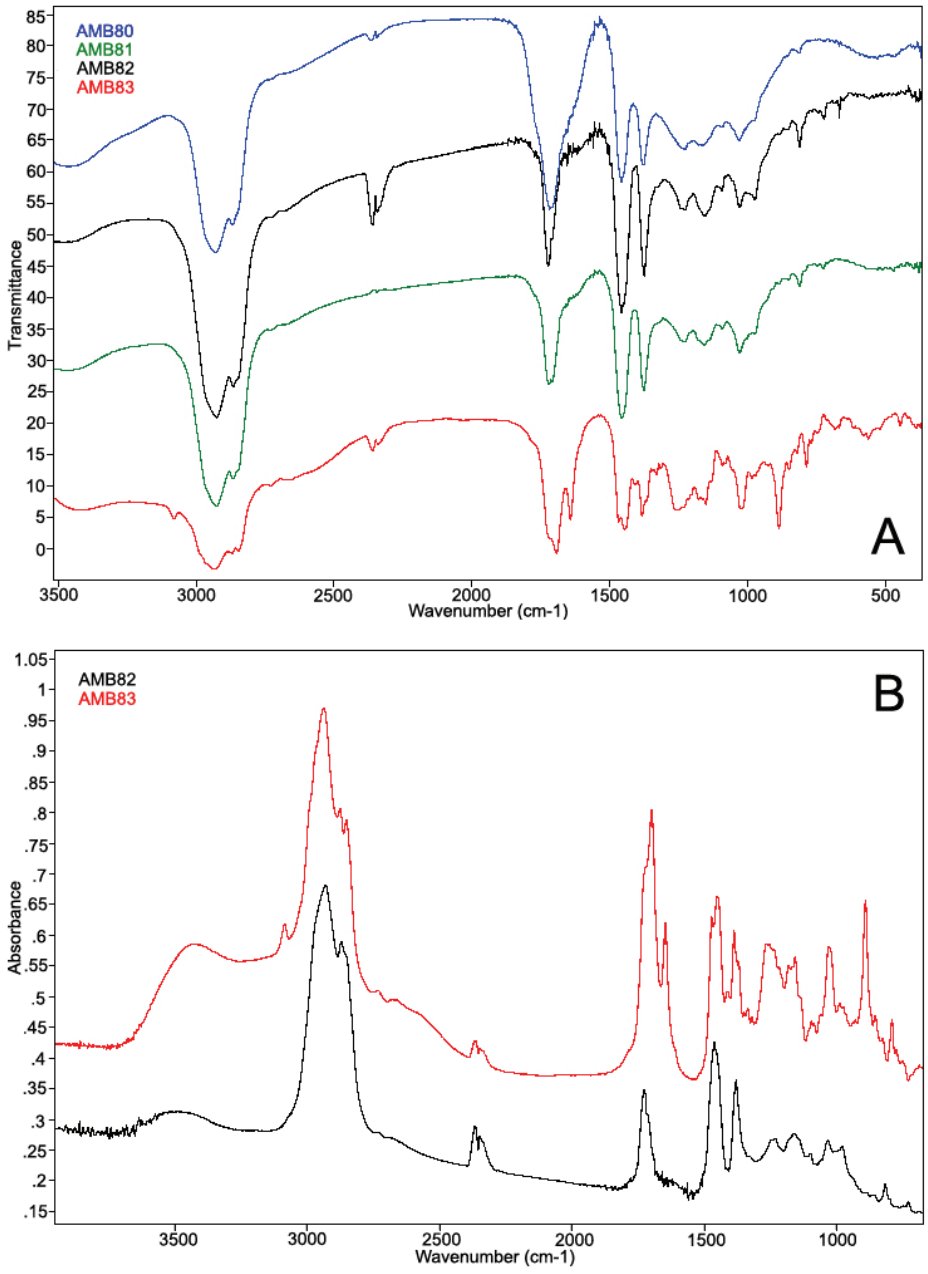

FIGURE 10 | **A) Transmittance IR spectra of El Soplao amber: AMB80 red amber from a kidney-shaped mass found within sands; AMB81 orange amber from a kidney-shaped mass found within clays; AMB82 orange amber from a stalactite-shaped flow, found within clays; and AMB83 dry resin from an *Agathis australis* stalactite-like flow, New Zealand in origin. B) IR absorbance spectra from the El Soplao amber and dry resin of *Agathis australis*, both samples analysed came from stalactite-shaped flows.**

When the IR absorbance spectra is compared between the amber sample AMB82, an aerial stalactite, and the sample AMB83, a fragment of recent stalactite of the araucariacean *Agathis australis* (Fig. 10), numerous differences may be observed. However, without GC-MS studies, the origin of the variable intensity and the presence of several bands cannot be possibly known. The presence of the absorption maximum in the single-band around 3081 cm^{-1} is typical in *Agathis* resin; however, it is typically absent in amber due to the polymerization of the resin and increasing maturity. In addition, the spectra around range bands 1650-1700 cm^{-1}, corresponding to the carboxyl groups, is very different between the amber and the resin. The intensity of absorption at wave-numbers 3400 and 1700 cm^{-1} decreases according to an increase in the maturity level of the samples. Other bands observed constitute an unresolved group near wave number 2930 cm^{-1} (C-H st), the most intense group band known for all Cretaceous spectra.

FOSSIL RECORD

Plant cuticle compressions

Exceptionally well preserved plant cuticle compressions are very abundant in the El Soplao amber deposit (Fig. 11), sometimes accumulating in levels up to 10 cm thick. The palaeobotanical samples taken from these levels also show amber and woody fragments, but at less percentage than plant-cuticle compressions (Figs. 11A-11D). Amber pieces show various shapes and colours from yellow to red (Fig. 11A), whereas unidentified, small, dark, woody fragments are preserved as spheroidal, charcoalified masses or charcoals (Fig. 11B). Cuticle fragments of the conifer *Frenelopsis*, of the extinct family Cheirolepidiaceae (Gomez et al., 2002), are the most numerous plant-cuticle components (Fig. 11C). These coniferous axes typically constitute cylindrical internodes bearing apically a nodal whorl of three leaves (Fig. 11E). Some *Frenelopsis* sp. cuticles also show a particular branching of axes borne in the internode (Fig. 11F) (see Daviero et al., 2001 for architectural details). A female cone scale formed by several layers of very thin cuticle (Fig. 11P) constitutes a doubtful record of the genus *Alvinia* Kvaček (Kvaček, 2000), associated with *Frenelopsis* vegetative material. Additionally, the conifer *Mirovia* sp. of the extinct family Miroviaceae (Gomez, 2002) shows about the same quantity of leaf cuticle fragments (Fig. 11D). The leaves clearly display a white central line on one side corresponding to the single middle stomatal-bearing groove, as well as a mucronate apex and suction-pad-shaped base (Figs. 11G-11H). Such leaves have been also described from the Albian of Pyrenees (Corça) and Teruel (Rubielos de Mora) (Gomez, 2002). Also present are two conifer leafy axes of *Brachyphyllum*-type with tiny, helicoidally arranged leaves (Figs. 11L-11M). In addition, two types of ginkgolean leaves also occur. *Nehvizdya* sp. shows obovate leaves with variable apex shapes (Fig. 11I) and attenuate base (Fig. 11J) (Gomez et al., 2000). The venation pattern showing several successive dichotomies and the presence of resin bodies between the veins are clearly seen in the most transparent leaves. In Spain, *Nehvizdya penalveri* has been reported only from the Albian of Rubielos de Mora in Teruel (Gomez et al., 2000). Other ginkgolean leaves are represented by *Pseudotorellia* sp. It has narrow leaves with three stomatal bands located on one side (Fig. 11K). This genus has also been described from the Albian of Rubielos de Mora in Teruel (Gomez, 2000). In addition, it has distinctive reproductive organs similar to the genus *Nehvizdyella* Kvaček (Kvaček et al., 2005), which probably are ovules associated with *Nehvizdya* (Figs. 11N-11O).

Arthropod inclusions

Until now, the arthropods found as inclusions in the El Soplao amber have been spiders and insects. All specimens are small in size, less than 1 cm long, and are well preserved, possessing slight deformation due to pressure. Apparently, the degree of maturation of the amber is slightly higher than the San Just and Álava ambers, because the external surface of the insects is dark, without a silvery gaseous film. That film produces silver-hued reflections under strong direct illumination and makes the appreciation of microsculptural details easier. Formal taxonomy of the new taxa of arthropods will be published elsewhere, principally by Paul Selden and one of us during the completion of a Doctoral Thesis (R.P.F.). Thus, only a brief overview of the most important specimens is presented below.

One of the most remarkable finds is a virtually complete spider specimen. The excellent preservation of the legs shows detailed structure of the tarsal claws (Fig. 9E). The tarsi have large, pectinate paired claws with one row of nine teeth and one small, non-pectinate median claw and numerous serrate bristles, similar to the Araneoidea specimen described by Selden (1989) from the Early Cretaceous limestones of El Montsec (Lleida Province, northeastern Spain). Subsequently, the Montsec specimen was described as *Cretaraneus vilaltae* by Selden (1990) and assigned to the orb-weaver family Tetragnathidae by Selden and Penney (2003). The characteristic claw morphology is structured for an efficient handling of silk and locomotion on an aerial web. Peñalver et al. (2006) published the oldest web with entrapped preys, most likely an orb web, from San Just amber. Penney and Ortuño (2006) described a spider from Álava amber, which displays three tarsal claws and accessory setae, as the oldest true orb-weaving spider, but without illustration and more detailed description of this crucial structure. Also, from the El Soplao amber, a portion of an aerial spider web was found (Fig. 9F), which trapped a small wasp of the family Megaspilidae. This new spider web has a different structure than the specimen from San Just amber. Both the spider specimen and aerial web found in the El Soplao amber shed light on and support the role of aerial webs in the palaeoecology of Cretaceous forests discussed by Peñalver et al. (2006, 2008).

The insect orders found to date in this new site also are the most abundant in other Cretaceous deposits (Fig. 12). These co-occurring orders are Thysanoptera (Fig. 12A), Hymenoptera (Fig. 12B), Blattaria (Fig. 12D), Hemiptera, Coleoptera, and Diptera; the last two are especially plentiful (Figs. 12C-12D). Raphidioptera and Neuroptera have a scarce record in El Soplao as is common in Cretaceous ambers.

Hymenopterans were represented previously by the families Scelionidae (Figs. 12B and 12D), Mymarommatidae, and Megaspilidae (Fig. 9A). The extinct family

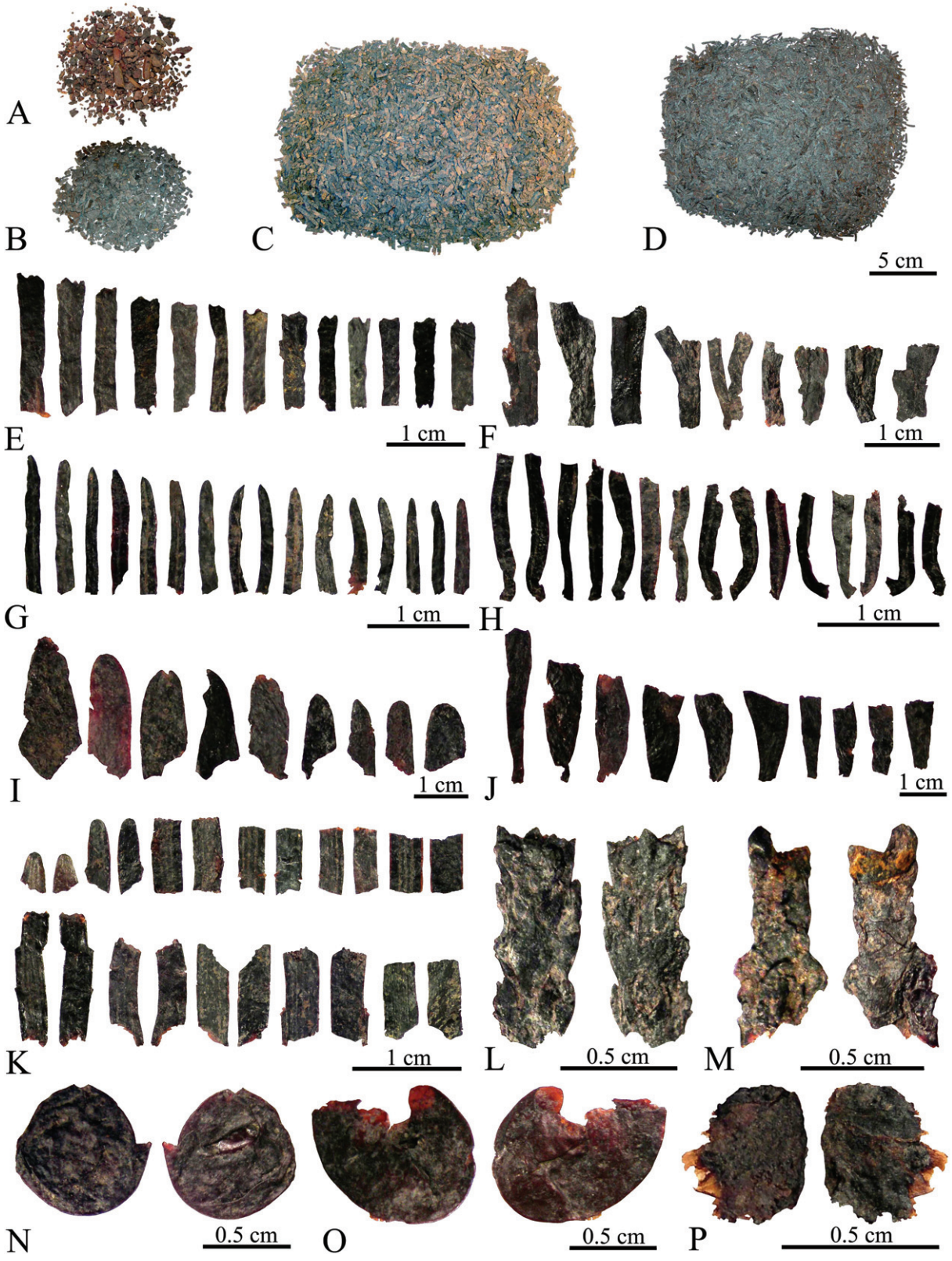

FIGURE 11 | **A, D) Four major palaeobotanical components sorted out from a sediment sample (all to the same scale). A) Yellow to red amber pieces. B) Wood fragments. C) *Frenelopsis* sp. cuticles. D) *Mirovia* sp. cuticles. E, F) Internodes of *Frenelopsis* sp. E) Apical nodal whorl of three leaves. F) Intra-internodal branching of axes. G, H) Leaves of *Mirovia* sp. G) A single middle stomatal groove and a mucronate apex. H) Suction-pad-shaped base. I, J) Leaves of *Nehvizdya* sp. I) Variable shapes of apices. J) Attenuate bases. K) Leaves of *Pseudotorellia* sp., showing two apices and three or more stomatal bands on one side of the leaves. L, M) Two *Brachyphyllum*-type leafy axes, showing small, helicoidally arranged leaves. N, O) Ovules of cf. *Nehvizdyella* sp., P) cf. *Alvinia* sp., a multilayered female cone scale of *Frenelopsis* sp.**

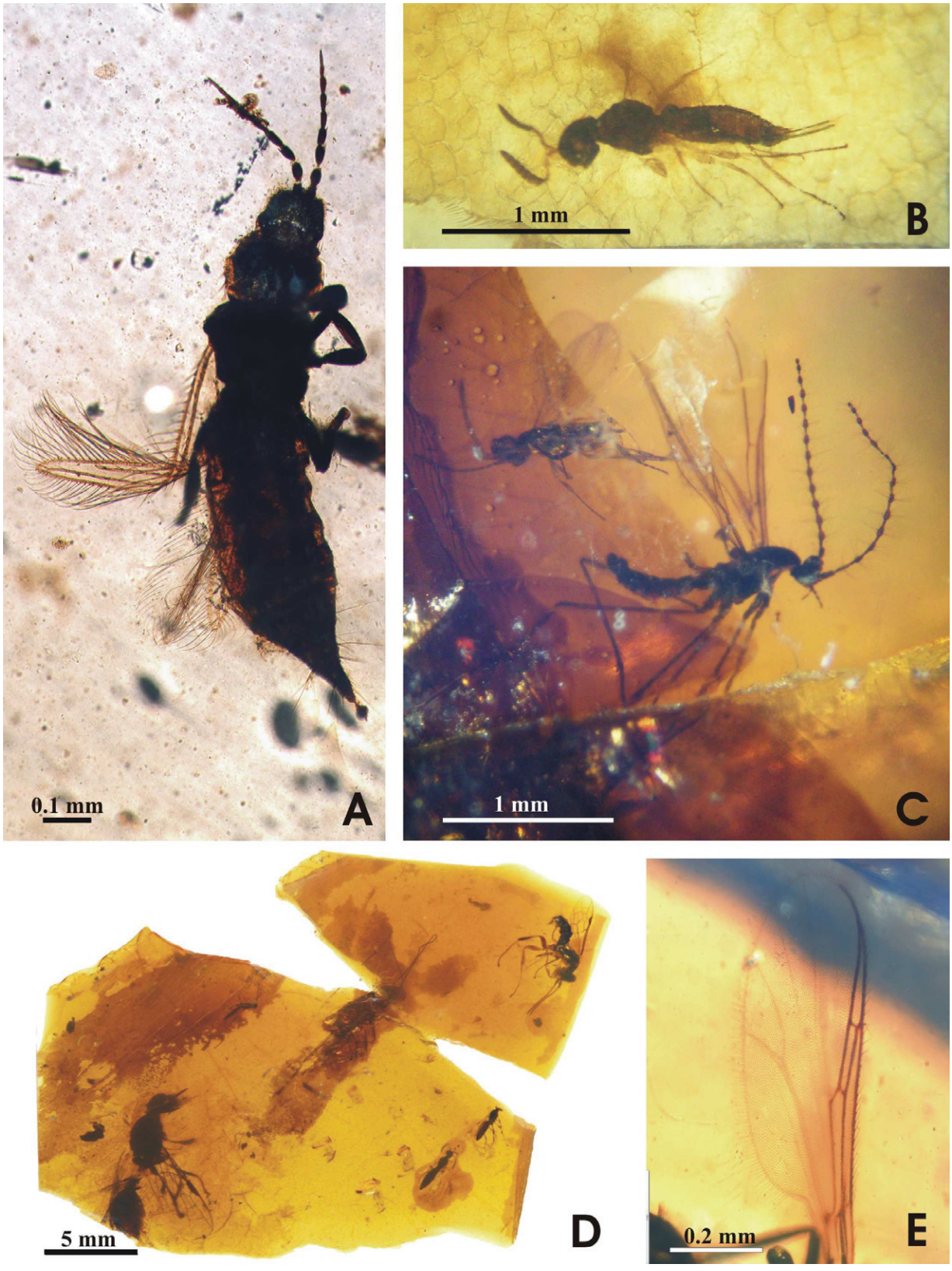

FIGURE 12 | **Fossil insects as bioinclusions in El Soplao amber. A) Thysanopteran specimen. B) Female wasp of the family Scelionidae. C) Chalcidoidean wasp -top- and dipteran of the family Cecidomyiidae (gall midges). D) Amber fragment with seven wasps and one immature cockroach in the centre of the preparation. E) Wing of *Archiaustroconops* sp. Images A and E were made with integrated consecutive pictures taken at successive focal planes.**

Mymarommatidae, or false fairy wasps, are among the smallest of Hymenoptera and constitute a very important record for the El Soplao amber, represented by a complete winged female of a new morphotype of the extinct genus *Archaeromma*. The family includes only five genera, three extant and two extinct genera (Gibson et al., 2007). The fossil record of this family is very scarce and is only preserved in amber. The genus *Archaeromma* contains eight species (Gibson et al., 2007; Engel and Grimaldi, 2007). This group of minute wasps is characterized by having a head capsule with a hyperoccipital band of pleated membrane separating the frontal plate from the flat occipital plate; an occipital foramen originating at ventral margin of occipital plate; mandibles exodont; female antennae with 6 or 7 funicular segments and 3 or 4 larger distal segments which form a compact tube; and other characters (Gibson et al., 2007). Due to their small size and unusual morphological characters, they are suspected egg parasitoids. The new record from the El Soplao amber is the oldest for this genus.

Among the most interesting insect records in the El Soplao amber are biting midges (Diptera: Ceratopogonidae). The genus *Archiaustroconops*, of the subfamily Austroconopinae, is the only Cretaceous Ceratopogonidae with two well-developed radial cells, an oblique r-m vein (Fig. 12E), and a foreleg/hindleg tarsal ratio ≥ 1.4 (Borkent, 2000). The genus includes six species known only from Lower Cretaceous Lebanese and Álava ambers (Borkent, 2000). It is represented in the El Soplao amber by one new morphotype (Fig. 12E), clearly different from *A. alavensis* found in Álava amber. This new morphotype is characterized by having a strongly elongate first radial cell. Most interesting is the presence of a new taxon of the rare genus *Lebanoculicoides* (Fig. 13), which is only known by two specimens described as *L. mesozoicus* from Lebanese amber (Szadziewski, 1996). This genus is the only member of the Ceratopogonidae having a wing with fully developed R1, R3 and R4+5 veins. This character, among others, indicates that *L. mesozoicus* is the sister group of all other Ceratopogonidae and for that reason it had been included in its own subfamily, named Lebanoculicoidinae by Borkent (2000). The new morphotype differs mainly from the other known species by having ovoidal flagellomeres (not cylindrical) and R4+5 vein terminating in a basal position before reaching the wing apex.

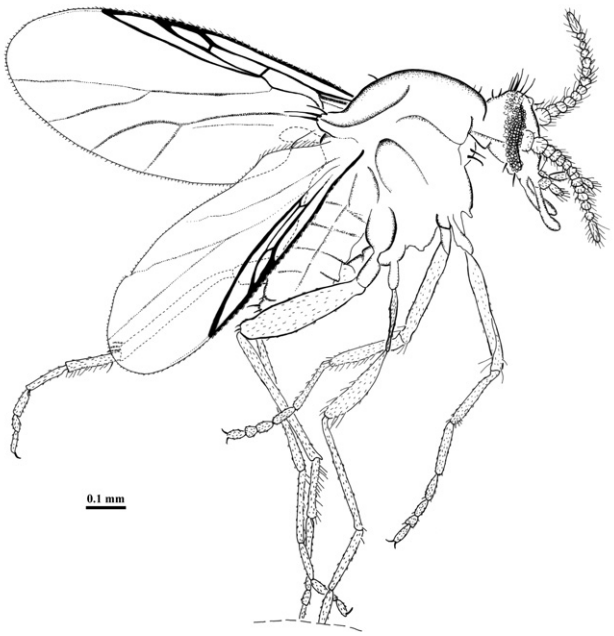

FIGURE 13 | **Camera lucida drawing of *Lebanoculicoides* sp. (Ceratopogonidae: Lebanoculicoidinae) in lateral habitus, from the El Soplao amber.**

DISCUSSION AND CONCLUDING REMARKS

Stratigraphic and sedimentologic analyses of the amber-bearing deposit of the Lower Albian Las Peñosas Fm. indicate that it was deposited on a regressive deltaic-estuarine environment. Facies associations are assigned to three different depositional units (P1 to P3). The stacking of these units and their internal vertical and lateral relationships resulted from an overall marine regressive phase followed by a transgressive marine phase, with the resin accumulation occurring at the most regressive part of the regressive-transgressive sequence (Unit P2). Sedimentological analysis of this unit suggests that the amber deposit constitutes part of the infilling of interdistributary bays, which are laterally associated with distributary meandering channels. The amber-rich beds always contain abundant fragments of carbonaceous material, wood fragments and leaves that still preserve the vegetal textures. The amber-rich beds appear associated with laminated, organic clays, but also with discontinuous beds of massive to laminated sandstones and siltstones with disorganized fragments of woody material. These deposits also contain shells of marine and/or brackish-water molluscs, which suggest a littoral to coastal marsh environment of deposition. Therefore, the suggested depositional scenario for the amber-rich beds is an environment of low-energy coastal and interdistributary bays connected with the sea and affected episodically by higher-energy conditions. Floods during rainstorms eroded and removed the amber and plant remains from their original place of accumulation at the soils of the coast-fringing forest. Then, the amber and plant fragments were transported by density flows that carried large amounts of these materials, mixed with mud and sand, to the coastal and interdistributary bays, where were rapidly accumulated and buried. Most

of the amber pieces show their original form of subrounded and stalactite-shape suggesting little erosion during transport. A remarkable characteristic of this amber deposit is the unusual accumulation of aerial amber pieces that contain abundant arthropod and other bioinclusions.

The El Soplao deposit likely originated during a period of abundant production of fluid resin within the palaeoforests, possibly coinciding with a warmer episode. The plant-cuticle assemblage of the El Soplao deposit is quite reminiscent of that from the Albian of Rubielos de Mora (Teruel Province); (Gomez, 2000, 2002; Gomez et al., 2000, 2002). However, the latter deposit has poorly preserved amber and identification at the species level is tenuous, lacking the precision for any determination of amber production. Araucariacean trees are the suggested resin-producing plants during the Cretaceous (Alonso et al., 2000; Chaler and Grimalt, 2005), but leaf remains of this group of conifers are absent from the El Soplao assemblage, although they occur in other similar Spanish deposits. Future palynological studies will complete our understanding of the palaeobotanical context of this deposit.

The abundance of fossil insects in the Early Cretaceous amber of El Soplao is particularly important for further evolutionary studies and palaeoecological reconstructions. This abundance is a consequence of the unusual concentration of amber flows (stalactite-like amber flow pieces and crusts), which contain the most bioinclusions. The fidelity of the arthropod preservation in this amber allows for detailed studies of the ancient forest biota, similar to other Spanish ambers. The Albian age of the El Soplao amber also is of particular importance because during this period certain groups of insects were diversifying to become major pollinators of the first flowering plants. In this context, the presence of spiders and their entrapping aerial webs in El Soplao amber reinforces the hypothesis advocated by Peñalver et al. (2006, 2008) which associates the diversification of spiders to the radiation of winged (pterygote) insects.

Several insect specimens recorded from the El Soplao amber are very scarce in the fossil record, for instance wasps and dipterans. Such is the case for the wasp specimen that belongs to the extinct family Mymarommatidae. Discovery of a new form of the rare dipteran *Lebanoculicoides* in the El Soplao amber indicates that this basal genus had a much more extensive distribution than previously supposed during the Early Cretaceous. Consequently, any new findings of fossil representatives of these groups would be of particular interest.

The FTIR spectra of the El Soplao amber are quite similar to other previously studied Spanish Cretaceous ambers. However, further investigations are necessary to complete the study of this new locality, including the taphonomic study of the deposit in order to know its origin, the palynological analysis of the amber-bearing stratigraphic sequence, determination of plant species represented as cuticles, and the taxonomic study of the arthropods included within the amber.

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Anexo I.2

A review of the El Soplao amber outcrop, Early Cretaceous of Cantabria (Spain)

Revisión del yacimiento de ámbar de El Soplao, Cretácico Inferior de Cantabria, España

Referencia completa:

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Resumen:

El yacimiento de El Soplao (Cretácico Inferior), recientemente descubierto en el Norte de España (Cantabria), es el mayor yacimiento de ámbar con inclusiones artropodianas hallado en España hasta la fecha. Datos importantes aquí proporcionados sobre la biogeoquímica del ámbar, palinología, tafonomía y bioinclusiones artropodianas complementan los datos previamente publicados. Estos nuevos datos sugieren, al menos, dos fuentes botánicas para el depósito de ámbar de El Soplao. El primer tipo de ámbar (tipo A) apunta a un origen relacionado con Cheirolepidiaceae, mientras que el segundo tipo (tipo B) muestra biomarcadores de conífera no específicos. La comparación de la composición molecular del ámbar tipo A con las hojas de *Frenelopsis* (Cheirolepidiaceae) indica una afinidad bioquímica y un origen botánico común. Un estudio palinológico preliminar muestra una diversidad taxonómica regional elevada, principalmente de esporas de pteridofitas y granos de polen de gimnosperma. Según los datos palinológicos preliminares, la región se hallaba habitada por bosques de conífera adaptados a la estación seca bajo un clima subtropical. La abundante madera carbonificada asociada a los mismos niveles de ámbar es una evidencia de paleoincendios que muy seguramente promovieron tanto la producción de resina como una intensa erosión del suelo, y la posterior acumulación de ámbar y cutículas vegetales. Además, fibras vegetales carbonificadas se describen como bioinclusiones por primera vez en el registro fósil. Otros datos tafonómicos relevantes son la presencia excepcional de serpúlidos y briozoos en las superficies de algunas piezas de ámbar, indicando una larga exposición a aguas marinas o salobres y un depósito mixto de ámbar, con historias tafonómicas dispares. Finalmente, se dan a conocer nuevos hallazgos de bioinclusiones de insectos, algunos de ellos infrecuentes en el registro fósil o mostrando notables adaptaciones. En conclusión, se proporciona una visión documentada del origen del yacimiento de ámbar de El Soplao.

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Review of the El Soplao Amber Outcrop, Early Cretaceous of Cantabria, Spain

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Abstract: El Soplao outcrop, an Early Cretaceous amber deposit recently discovered in northern Spain (Cantabria), has been shown to be the largest site of amber with arthropod inclusions that has been found in Spain so far. Relevant data provided herein for biogeochemistry of the amber, palynology, taphonomy and arthropod bioinclusions complement those previously published. This set of data suggests at least two botanical sources for the amber of El Soplao deposit. The first (type A amber) strongly supports a source related to Cheirolepidiaceae, and the second (type B amber) shows non-specific conifer biomarkers. Comparison of molecular composition of type A amber with *Frenelopsis* leaves (Cheirolepidiaceae) strongly suggests a biochemical affinity and a common botanical origin. A preliminary palynological study indicates a regional high taxonomical diversity, mainly of pteridophyte spores and gymnosperm pollen grains. According to the preliminary palynological data, the region was inhabited by conifer forests adapted to a dry season under a subtropical climate. The abundant charcoalified wood associated with the amber in the same beds is evidence of paleofires that most likely promoted both the resin production and an intensive erosion of the litter, and subsequent great accumulation of amber plus plant cuticles. In addition, for the first time in the fossil record, charcoalified plant fibers as bioinclusions in amber are reported. Other relevant taphonomic data are the exceptional presence of serpulids and bryozoans on the surfaces of some amber pieces indicating both a long exposure on marine or brackish-water and a mixed assemblage of amber. Lastly, new findings of insect bioinclusions, some of them uncommon in the fossil record or showing remarkable adaptations, are reported. In conclusion, a documented scenario for the origin of the El Soplao amber outcrop is provided.

Key words: fossil resin, chemotaxonomy, paleobotany, charcoal, arthropod bioinclusions, taphonomy, Early Albian

1 Introduction

Amber preserves delicate organic fossils, including microorganisms, cells and tissues, but the most abundant record is constituted by insects, sometimes showing interactions between them, such as mating interaction, commensalism and parasitism (e.g. Grimaldi, 1996; Martínez-Delclòs et al., 2004; Grimaldi and Engel, 2005). Early Cretaceous amber is remarkably important, because it was during this period that there occurred explosive radiations of the flowering plants and many modern families of insects (Grimaldi and Engel, 2005). During the last decade several new deposits of Cretaceous amber have been discovered in Spain and France (e.g. Delclòs et al., 2007; Perrichot and Néraudeau, 2009), and researches on various aspects of Cretaceous amber have increased greatly. However, most of the researches made concern the taxonomical descriptions of arthropods and microorganisms embedded in amber. Only a few studies have been conducted on the origin of both the amber and the deposits that contain it. One of the most

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important aspects concerning Cretaceous amber is the plant source, if there was only one, but this aspect has been shown to be very difficult to ascertain with confidence.

The first detailed description of Spanish amber was published by Casal (1762). Approximately 150 years later Boscá (1910) first indicated the possible presence of insects preserved in Spanish amber. After the discovery of two remarkable amber deposits rich in bioinclusions, Peñacerrada I in the north and San Just in the north-east of Spain, a third major amber deposit was discovered in 2008 in Cantabria, named El Soplao. Thus it was not included in the most recent review of Spanish amber outcrops by Delclòs et al. (2007). Najarro et al. (2009) described in detail the regional geology, the features of the amber pieces, including infrared spectroscopy analyses, and a first attempt of the bioinclusions and the plant cuticles associated with the amber. Subsequent papers deal with biogeochemistry of amber and descriptions of new arthropod taxa preserved as bioinclusions. Thus, Menor-Salván et al. (2009a, 2009b) investigated biomarkers from amber pieces and *Frenelopsis* leaves from the El Soplao outcrop, concluding that they share the same origin; in addition, they identified the chemical compound form that produces an intensive fluorescent blue glow when this amber is under normal sunlight. More recently, Menor-Salván et al. (2010) report some paleochemotaxonomical aspects of the biological diterpenes preserved in El Soplao amber. On the other hand, Pérez-de la Fuente et al. (2010) and Nel et al. (2010) described the new insect taxa *Cantabroraphidia marcanoi* (Raphidioptera: Mesoraphidiidae) and *Tethysthrips hispanicus* (Thysanoptera: Thripidae), respectively. Lastly, Ortega-Blanco et al. (2010a) report the fauna of false fairy wasps (Mymarommatoidea) that has been recorded in Spanish Cretaceous amber, including a paratype specimen from El Soplao amber.

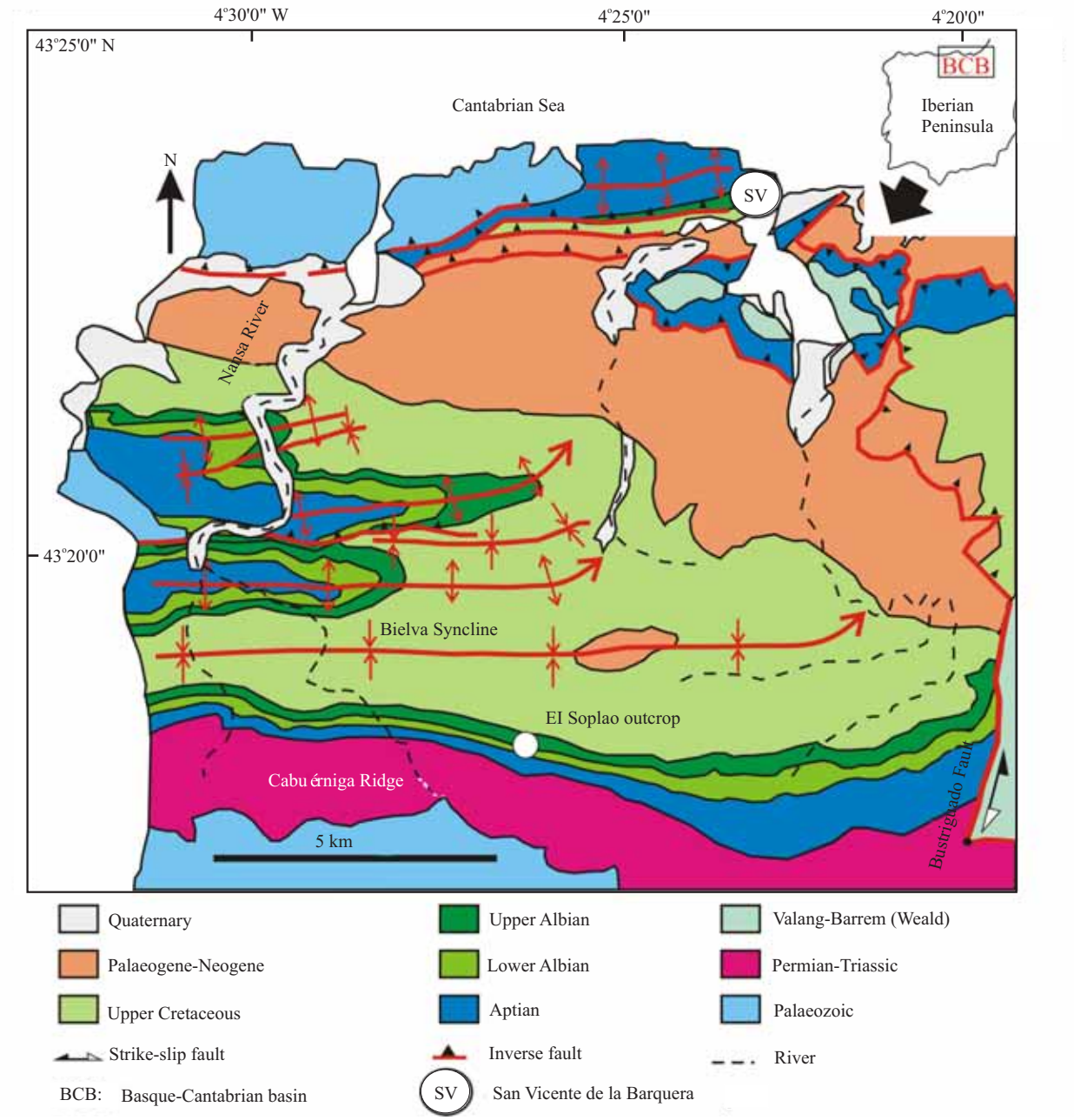
We report relevant new data about El Soplao amber deposit, such as new detail on stratigraphy of the amber-bearing levels, new geochemical and biogeochemical information of the amber and fossil leaves, palynological data, the presence of a great abundance of charcoal associated with the amber, the presence of marine invertebrates on the surface of some amber pieces and new discoveries about the bioinclusions. These new contributions permit us to portray a more documented scenario for the origin of the El Soplao amber outcrop.

2 Geology

The El Soplao outcrop belongs to the Cretaceous succession of the north-western margin of the Basque-Cantabrian Basin. During the Cretaceous, this basin was affected by extensional tectonics, and perhaps strike-slip, associated with the opening of the North Atlantic Ocean and the Bay of Biscay (e.g. Le Pichon and Sibuet, 1971; Rat, 1988; García-Mondéjar et al., 1996; Soto et al., 2007). During the Late Jurassic–Early Cretaceous a major rift phase developed that led to the formation of several narrow sub-basin controlled by E–W, NW–SE and SW–NW trending faults, in which variable thicknesses of continental to marine sediments accumulated (García-Mondéjar et al., 1996; Soto et al., 2007). The El Soplao area lies in the North Cantabrian sub-basin located immediately to the north of the Cabuérniga Ridge (Wilmsen, 2005), which is an E–W late-Variscan structure reactivated first as a paleo-high bounded by normal faults during the Early Cretaceous, and later as a reversal fault during widespread Tertiary (Pyrenean) compression (Fig. 1). The Lower Cretaceous (Aptian–Albian) deposits of the El Soplao area lie unconformably on lower Triassic (Buntsandstein facies) basement. They constitute a relatively thin (~300 m) sedimentary wedge weakly deformed and affected only by gently folding. The El Soplao amber outcrop is located in the southern flank of the Bielva syncline (Fig. 1), where the average strike of the succession is E–W and the dip about 40º N.

Thermal maturity of the area based on vitrinite reflectance values (*% Ro*) performed on vitrinite macerals from plant fragments have yield relatively low reflectance values that range between 0.50% and 0.61% (mean 0.56%) (Menor-Salván et al., 2010). These values suggest that the organic matter associated with the amber is only early mature, and the estimated temperatures from these indices of thermal maturation of organic matter are in the range of 60–70ºC (e.g. Sweeney & Burnham, 1989), which are the burial maximum temperatures suffered by the amber deposit. These low maturity levels may be responsible for the good conservation of the molecular composition of the amber and its biological inclusions.

A synthesis of the stratigraphy of the Soplao area is represented in Fig. 2 (after Najarro et al., 2009, 2010). The amber-bearing deposit of El Soplao is included within the Las Peñosas Formation (Fig. 2), which is a Lower Albian unit (~112–110 Ma) of continental to transitional marine siliciclastic deposits interbedded in a succession of shallow marine, rudist and coral carbonate platform deposits. General sedimentary descriptions, depositional environments and fossil content of the Las Peñosas Formation have been already discussed in Najarro et al. (2009). In the El Soplao outcrop, the amber-rich beds occur in the lower-middle part of the Las Peñosas Formation. There, this unit rests disconformably above a thin (1–2 m) bed of continental red clay with root traces, deposited at the top of shallow marine limestones of the Reocín Formation (Fig. 2). The El Soplao amber deposit is characterized by dark, carbonaceous, pyritiferous shales with subordinated siltstones and sandstones laminae and cross-laminated centimetric sandstone layers, forming wavy and lenticular bedding. They contain remarkable accumulations of plant remains and amber pieces of different sizes and forms, as well as some remains and small shells of marine gastropods and bivalves. The principal amber-bearing shale bed of the El Soplao outcrop forms a lenticular body with maximum thickness of 1.5–2.0 m and a width of at least 10 m in N–S cross-section. In the strike of the bed, the amber-bearing shale extends more than 75 m. The base of this len-shaped shale bed is erosional and truncates highly bioturbated, medium to coarse-grained sandstones with cross-bedding. At its top, the amber-bearing shale bed is overlain by heterolithic carbonaceous sandstones and muddy siltstones to sandstones with flaser bedding, which are also relatively rich in amber pieces. All of these deposits accumulated in a proximal estuarine bay system with small bayhead deltas (Najarro et al.,



2009) and represent the transgressive inundation of a continental fluvial plain and an incised valley fill. Based on geometry and facies, we interpret the amber-bearing shale of the El Soplao outcrop to have accumulated in a restricted tidal channel with low circulation and anoxic bottom-water, as suggested by widespread early pyritization.

3 Methods

3.1 Paleontological excavations

Three paleontological excavations have been carried out in El Soplao amber outcrop. During the first one (October 2008) different extraction methods were applied to obtain amber pieces. Amber was obtained manually with small tools. In addition a large prospect hole, approximately 7 × 2.5 × 2 m in size, was dug in one of the amber-rich areas of the outcrop using a bulldozer. Several tons of amber-bearing sediment from the large prospect hole were transported to a washing area located in the same outcrop, where a cement mixer and a sieve were used to obtain all ranges of amber sizes as described in Corral et al. (1999) and Alonso et al. (2000). This permitted to obtain a sampling without taphonomic biases introduced by the extraction methods towards the large and medium sizes. During the last excavation (July 2009) additional small prospect holes were dug close to the limits of the outcrop to find lateral extensions of the amber deposit. This task showed a high abundance of amber and revealed that the amber bed is at least 75 m long laterally, supporting the assertion of Najarro et al. (2009), which is that the El Soplao is the largest site of amber with arthropod inclusions that has ever been found in Spain so far.

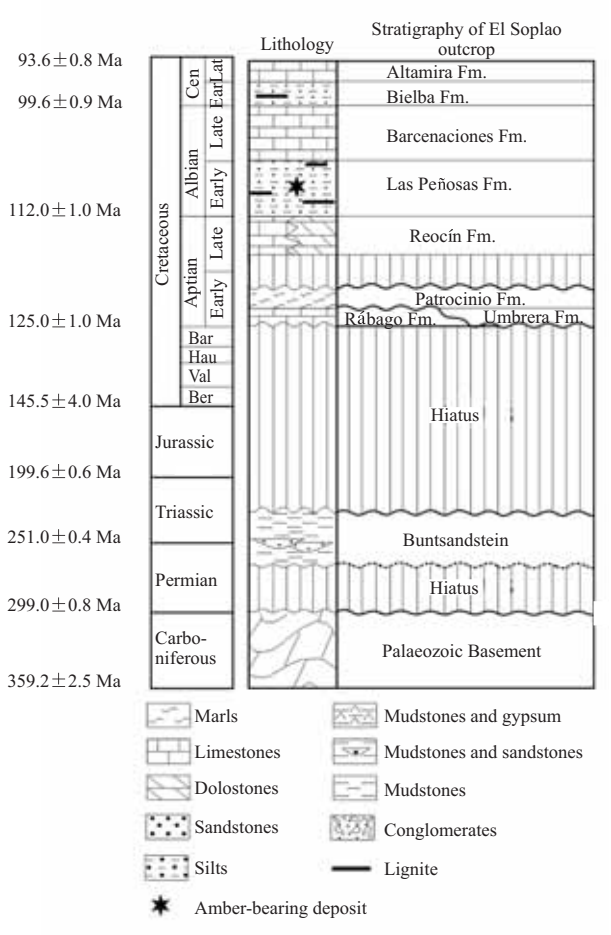


Fig. 2. Chrono- and lithostratigraphy of the El Soplao area.
Modified from Hines (1985) and Najarro et al. (2010). Chronostratigraphy after Gradstein and Ogg (2009).

During the second paleontological excavation (March 2009) a new method was used to obtain abundant amber material increasing the collection of bioinclusions. The technique involves the use of high pressure water (Fig. 3.1 and 3.2) to extract entire large amber pieces that would be too fragile to resist conventional methods (Fig. 3.3). The water at high pressure disintegrated the sediment of the prospect hole and exposed the amber pieces, which were manually extracted to avoid fracturing. On the other hand, the small and medium pieces were retained using a large sieve where water and mud flowed (Fig. 3.2). The pieces from the mixture of mud, plant cuticles, coal and amber retained by the large sieve were separated in the washing area described above. This high pressure water method used for the first time to extract amber is already used in mining to fragment mineral seams, and to extract the useful parts from the waste rock. In conclusion, the new method was useful in obtaining numerous large amber pieces in a short period of time.

3.2 Biogeochemical analyses

For the biogeochemical analysis amber pieces, fossil wood, and sediments rich in plant cuticles were collected from the El Soplao deposit during the first excavation on October 2008. Two types of amber pieces were collected: type A, characterized by a strong blue purple color under natural light (Fig. 3.3 and 3.4), purple-reddish under artificial light, and type B, less abundant, yellow under artificial light and with a bluish tinge under natural light. Plant cuticles were obtained from claystones by rinsing the plant-rich sediment in an ultrasonic bath of distilled water to remove all of the clay and silt sediment. The organic residue was air-dried. Plant fragments and leaves were distinguished and separated under a stereomicroscope. In addition, several resin and leaf samples from extant conifers of the families Cupressaceae and Araucariaceae (*Cupressus arizonica, Agathis australis* and *Araucaria angustifolia*) were collected from living trees at the Royal Botanic Garden of Madrid and in the kauri forests of New Zealand, in order to compare their compounds with those of the amber and fossil leaves and also to determine potential affinities of the amber with fossil taxa.

For the analytical characterization, several representative pieces of amber of the types A and B of about 50 g each, with the highest transparency available and free of major inclusions, crusts and debris, were selected from the El Soplao deposit. Following standard techniques, each piece was crushed and extracted for 4 h with dichloromethane:methanol (2:1) using a Büchi model B-811 automatic extractor. One aliquot of extract was injected directly into the injection port of the gas chromatograph. The bulk extract was concentrated to a volume of 20 mL and fractionated by use of flash chromatography on silica gel. The elution was carried out using hexane, dichloromethane, dichloromethane:methanol (1:1), and methanol, and subsequently 25 fractions were collected. Each fraction was concentrated by evaporation of the solvent under N_2 and analyzed by gas chromatography/mass spectrometry (GC/MS). The fractions with similar compositions were combined. The polar fraction (eluted with methanol) and the fractions containing ferruginol were recombined, further separated using a glass column (20 cm) filled with chromatographic-grade silica gel, and eluted sequentially with n-hexane:dichloromethane (1:1), pure dichloromethane, dichloromethane:methanol (1:1), and methanol. Four fractions were collected, designated A through D. All fractions were dried and the alcohols and acids converted to trimethylsilyl derivatives by reaction with N,O-bis-(trimethylsilyl)trifluoroacetamide (BSTFA) containing 1% trimethylchlorosilane (TMCS) at 65ºC for a period of 3 h. Finally, the derived fractions were diluted with n-hexane and injected into the port of the gas chromatograph.

To study the molecular composition of fossil *Frenelopsis* and *Arctopitys* leaves (genus name *Mirovia* changed to *Arctopitys*; see Nosova and Wcisło-Luraniec, 2007), 5 g of leaves were extracted for 4 h with dichloromethane:methanol (2:1) using a Büchi model B-811 automated extractor. The bulk extract was filtered and analyzed directly by gas chromatography-mass spectrometry. After, extract was fractionated using silica gel chromatography in two fractions by elution with hexane:dichloromethane (3:1) and dichloromethane:methanol (4:1). The polar fraction was dried and derived using the method described above. For comparison, the chemotaxonomy of extant Cupressaceae and Araucariaceae was

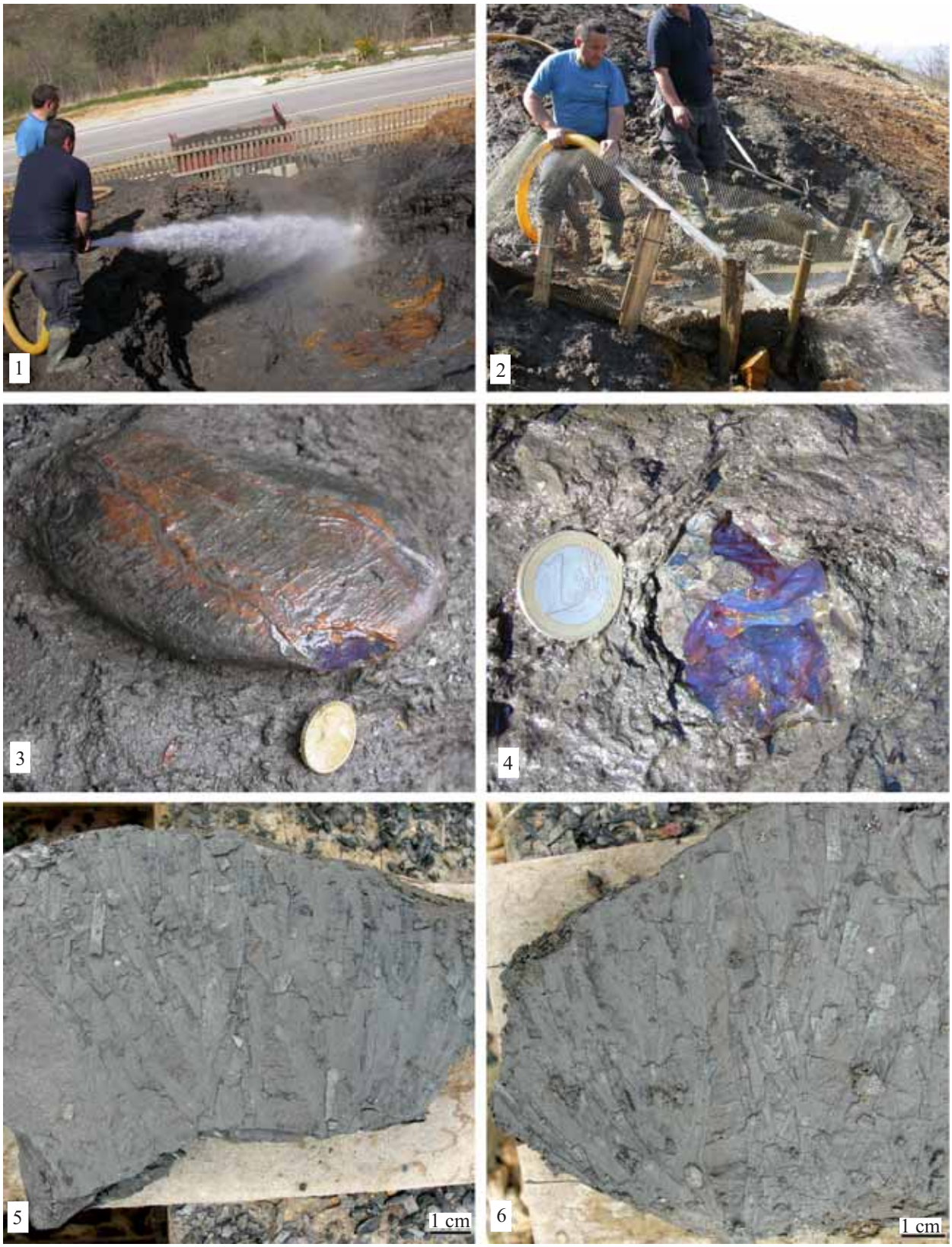


Fig. 3. Paleontological excavation in El Soplao amber outcrop (March 2009) with a new extractive method and some of the pieces obtained in situ.

1: High pressure water directed to the prospect hole; 2: large sieve to which water and mud flowed; 3: flattened amber piece virtually complete exposed *in situ* by high pressure water showing intensive fluorescent blue glow on its fracture (coin diameter 24 mm); 4: fragment of amber *in situ* showing intensive fluorescent blue glow (coin diameter 23 mm); 5–6: part and counterpart of four-time branched shoots of *Frenelopsis* sp. collected during the last excavation carried out (July 2009).

investigated using resin samples from *Cupressus arizonica*, *Agathis australis*, and *Araucaria angustifolia*. The resin was dissolved in dichloromethane:methanol (1:1) and fractionated by chromatography on silica gel in two fractions: the less-polar fraction being eluted with n-hexane:dichloromethane (1:4), and the second polar fraction being eluted with methanol. The polar fraction was dried under a nitrogen stream, yielding a white powder composed mainly of resin acids and highly polar compounds. The polar components were converted into trimethylsilyl derivatives by BSTFA and analyzed using GC-MS as described previously (Menor-Salván et al., 2010).

3.3 Palynological method

Two samples, Sop-Peñosas (this from the amber outcrop) and Peñosas-Cóbreces, both from Las Peñosas Formation, were prepared for palynological studies in the laboratory of ALICONTROL (Madrid, Spain). The rock samples were treated following the standard palynological preparation technique (Batten, 1999), which consists of an acid attack with HCl, HF and HNO_3 at high temperature. The residue was concentrated and sieved throughout sieves of different grid sizes (500, 250, 75, 50 and 12 μm). Then, the samples were mounted in glycerin jelly on glass slides for light microscopy. The samples were studied with an Olympus BX51 optical microscope. Both samples yielded representative and well-preserved assemblages: Sop-Peñosas yielded 488 miospores and Peñosas-Cóbreces 681 miospores.

3.4 Microscopic photography

Scanning electron micrographs of the charcoal were taken using a HITACHI model S-2500 of the University of Valencia. Optical photography used both a digital camera attached to a microscope Olympus BX51 and a digital camera Leica DFC420 attached to a stereomicroscope Leica MS5.

4 Biogeochemistry of the Amber

The overall aim of this part of the research was to identify the bioterpenoids preserved in the fossil resin and to determine their possible botanical source. Due to exceptional preservation, the amber-bearing deposit at El Soplao offers a unique opportunity to compare the molecular composition of the amber with that of the plant remains that appear in the same deposit.

The analysis of the polar terpenoids of the amber from El Soplao indicates that most likely at least two resin producers contributed to the amber record (Fig. 4). The main parent resin (type A; Fig. 4.1) originally contained phenolic abietanes (dominated by ferruginol), totarol, dehydroabietane and pimarane/isopimarane acids. The dominant resin acids found were 13-dihydroagatholic and bisnordehydroabietic acids, as well as various other alteration products and minor quantities of callitrisic acid and hinokiol. The second parent resin (type B; Fig. 4.2) shares some general compounds characteristic of conifers with type A amber, but shows remarkable differences in specific biomarkers. It contained pimarane/isopimarane acids as the only identifiable biological precursors preserved and shows absence of phenolic terpenoids (ferruginol, totarol, hinokiol) and other specific biomarkers that are present in type A amber (e.g. dehydroabietane, callitrisic acid).

The direct diagenetic products of the pimarane/abietane and labdane class terpenoids constitute the main geoterpenoids extractable from both types of El Soplao amber. The moderate degree of burial diagenesis of the studied material deduced from the low vitrinite reflectance values is consistent with the high level of preservation of the natural product diterpenoids and their direct diagenetic derivatives.

The preliminary molecular data obtained from the comparative study of the megafossil plant leaves, extant plant samples and the two amber types lead to the following results:

(a) There is absence of abietic and dehydroabietic acids in both types of amber samples. This allows us to reject a relationship between the amber and resin of Pinaceae species. Also, the absence of triterpenoids and labdatriene acids discards the contribution of angiosperms (Anderson et al., 1992; Yamamoto et al., 2006).

(b) In type A amber, the phenolic diterpenoids present in the analyzed samples and the absence of phyllocladane/kaurane type terpenoids discard the contribution of the family Araucariaceae. The presence of phenolic terpenoids (ferruginol, totarol and hinokiol) points to a relation with the extant conifer families Cupressaceae, Taxodiaceae and Podocarpaceae. However, the presence of dehydroabietane (also present in representatives of Pinaceae and Cupressaceae; Otto et al., 2007) points to a relationship with the family Cupressaceae. The presence of callitrisic acid in type A amber reinforces a biochemical relation between the parent resin of amber and modern Cupressaceae, because in modern conifer resins the synthesis of callitrisic acid seems to be restricted to certain genera of Cupressaceae (Anderson, 2006). The analysis of the molecular composition of fossil leaves from the same outcrop shows the presence of key terpenoids, such as ferruginol, in both type A amber and the analyzed *Frenelopsis* fossil leaves, suggesting that this amber could be derived from the genus *Frenelopsis* (Cheirolepidiaceae). For the type A amber, a possible diagenetic route is suggested in Fig. 5 that connects the preserved biological precursors and the major geoterpenoids found in the sample (Otto and Simoneit, 2002; Stefanova et al., 2002; Hautevelle et al., 2006; Pereira et al., 2009). Morphological similarities between extinct Cheirolepidiaceae and extant Cupressaceae has been already described, but their phylogenetic relationship remains speculative, mainly due to the lack of molecular evidence (Seoane, 1998; Miller, 1999; Farjon, 2008); there are also paleobotanical data that support close affinities between Cheirolepidiaceae and Araucariaceae mainly based on female cone morphology. The chemotaxonomical affinity between type A amber and the analyzed leaves of *Frenelopsis* (Cheirolepidiaceae), and the affinity between type A amber and Cupressaceae as well, strongly suggests biochemical affinity between the extinct *Frenelopsis* and the modern representatives of the family Cupressaceae.

(c) The overall terpenoid composition of B samples (Fig. 4.2) is represented by non-specific conifer biomarkers. Absence of

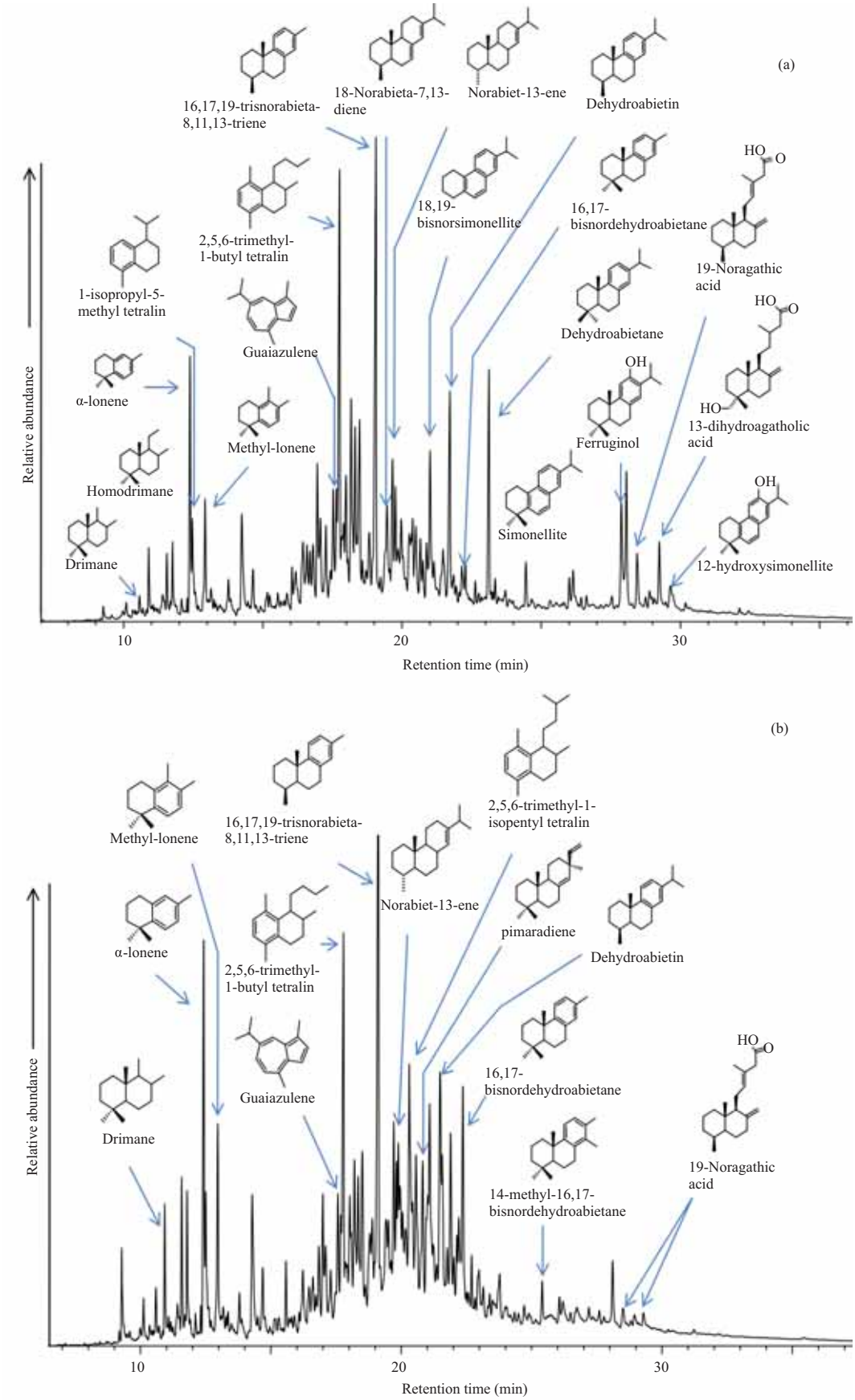


Fig. 4. Gas chromatography-mass spectrometry traces (TIC) analysis and main biomarkers identified in the two types of amber found at El Soplao deposit: type A (a) and type B (b). After Menor-Salván et al. (2010).

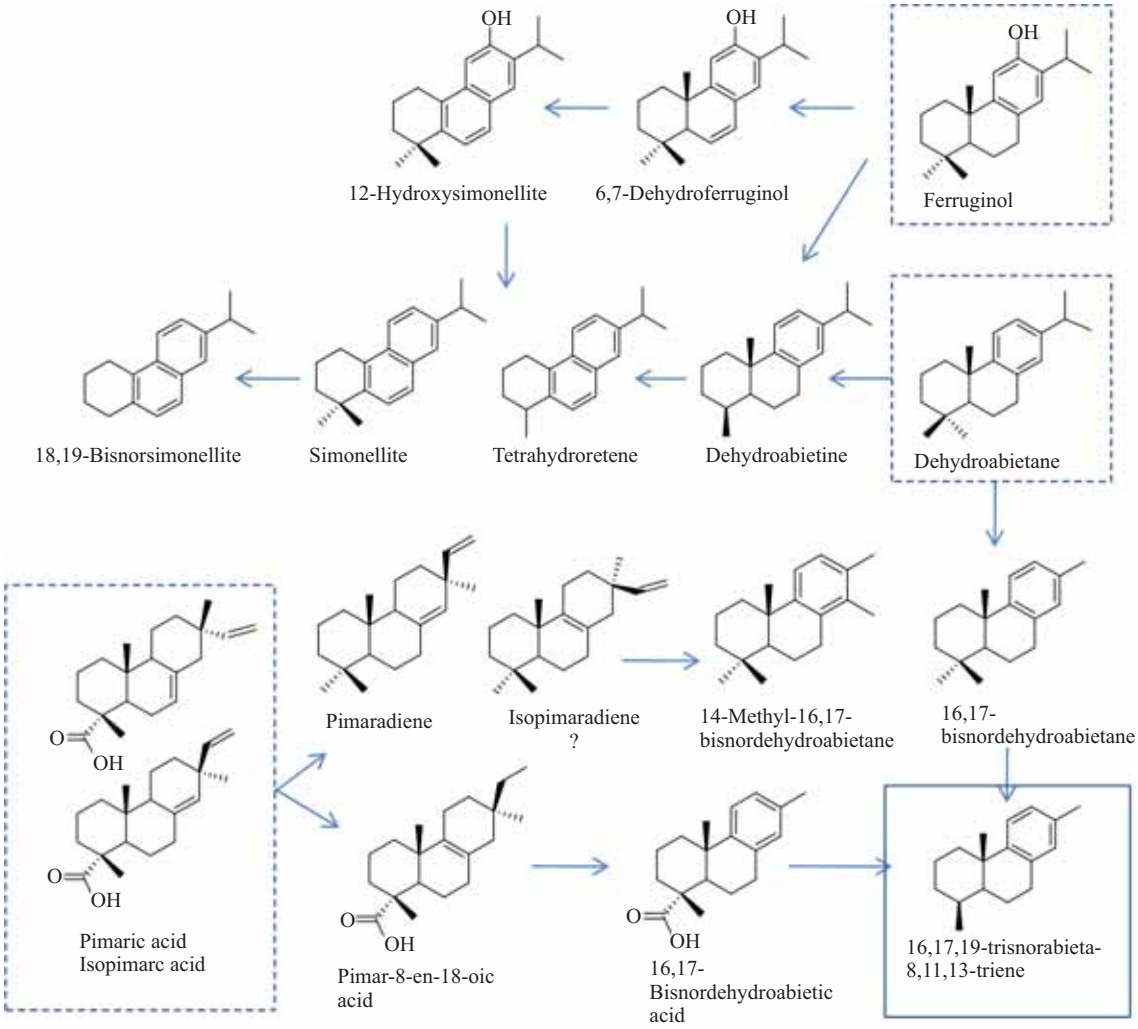


Fig. 5. Diagenetic pathways proposed for the El Soplao amber.
Dotted box: biological precursors. After Menor-Salván et al. (2010).

phenolic terpenoids and 13-dihydroagatholic acid, together with a major presence of diagenetic products of pimarane type terpenoids, saturated and unsaturated norabietanes and alkyltetralines in B samples, points to a different biological origin. Paleobotanical source for this type of amber could not be identified on the basis of the biomarker composition found so far.

Although these results are preliminary and might change when more data become available from analyses of more samples, it is estimated that they already provide a good indication of the potential plant source that originated the El Soplao amber. Future analyses could include fossil wood, leaf cuticle of *Nehvizdya*, more amber samples and conifer resin samples of other taxa.

5 Palynology

This preliminary palynological study complements that based on plant cuticles from the amber outcrop (see Najarro et al., 2009), revealing some additional aspects of the regional paleobotany. The studied samples from Las Peñosas Formation have yielded 32 spore and 29 pollen types (Fig. 6; see Table 1). In addition, undetermined bad-preserved dinoflagellate cysts and lining of foraminifera scarcely occurred. The Peñosas-Cóbreces sample presents more abundant taxa (52) than the Sop-Peñosas sample (44). It may be related to a lower palynological richness in the second sample. Both samples present high percentages of conifer pollen grains, especially those of *Classopollis* and *Inaperturopollenites dubius*. The spores of vascular cryptogams are more diverse than pollen grains although they occur in lower amounts. The most usual spores belong to both the trilete and taeniate genus *Cicatricosisporites* and the trilete and psilate genus *Deltoidospora*. Pollen grains of ancient angiosperms occur scarcely in both samples. They are mainly represented by monosulcate and reticulate pollen grains of the genus *Clavatipollenites*.

The Peñosas-Cóbreces sample exhibits high amounts of pollen grains of *Classopollis* (~40%) and *I. dubius* (~30%). Other gymnospermous pollen grains such as *Alisporites* spp., *Araucariacites australis*, *Monosulcites chaloneri* and *Spheripollenites* sp. present lower but remarkable percentages.

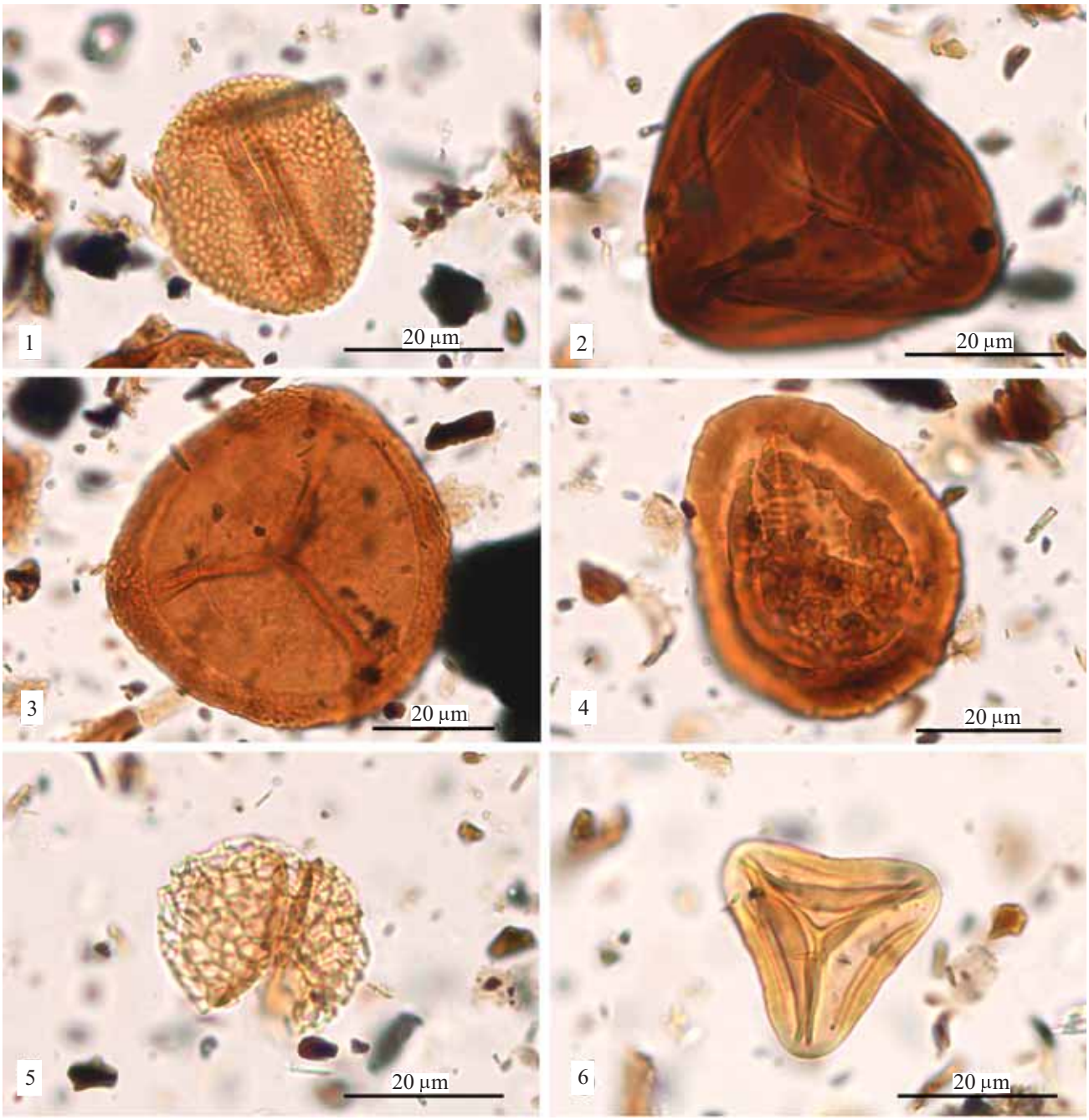


Fig. 6. Miospores from Peñosas-Cóbreces (1–5) and Sop-Peñosas (6) palynological samples.
1: *Liliacidites dividuus* (Pierce) Brenner; 2: *Cicatricosisporites patapscoensis* Brenner; 3: *Densoisporites velatus* Weyland & Krieger; 4: *Taurocosporites segmentatus* Stover; 5: *Pennipollis peroreticulatus* Brenner; 6: *Gleicheniidites senonicus* Ross.

Spores also present low amounts being *Cicatricosisporites* spp. the best represented (~2%). The occurrence of a single tricolpate pollen grain of the genus *Tricolpites* is noteworthy, because up to the Middle Albian this taxon is not abundantly represented.

The Sop-Peñosas sample corresponds to the El Soplao amber outcrop. The palynological assemblage inferred in this sample is characterized by a conspicuous increase in *I. dubius* (~51%) and a marked decrease in *Classopollis* (~11%). The percentage of spores of the genus *Deltoidospora* also increases (~8%). *Cicatricosisporites* scarcely occurs at this sample. Angiosperm pollen grains are low represented in this sample compared to Peñosas-Cóbreces.

From a biostratigraphical point of view, the occurrence of *Appendicisporites robustus* and *Cicatricosisporites patapscoensis* (Fig. 6.2) indicates a Late Aptian–Middle Albian age. However, the occurrence of *Liliacidites dividuus* (Fig. 6.1) and the low presence of *Tricolpites* sp. indicate an Early Albian age for the Peñosas-Cóbreces sample (Doyle and Robbins, 1977).

Table 1 List of spores and pollen grains recorded from the Early Albian sediments of Las Peñosas Formation

	Peñosas-Cóbreces	%	Sop-Peñosas	%
Spores				
Appendicisporites robustus Kemp 1970	1	0.147	0	0
Appendicisporites dentimarginatus Brenner 1963	0	0	2	0.410
Appendicisporites tricornitatus Weyland & Greifeld 1953	1	0.147	0	0
Appendicisporites spp.	2	0.290	1	0.205
Baculatisporites sp.	0	0	1	0.205
Biretisporites potoniaei Delcourt & Sprumont 1955	3	0.440	3	0.615
Ceratosporites sp.	1	0.147	0	0
Cibotiumspora jurienensis (Balme 1957) Filatoff 1975	0	0	1	0.205
Cicatricosisporites apicanalis Phillips & Felix 1971	1	0.147	0	0
Cicatricosisporites apitereus Phillips & Felix 1971	1	0.147	0	0
Cicatricosisporites patapscoensis Brenner 1963	1	0.147	0	0
Cicatricosisporites recticicatricosus Döring 1965	1	0.147	0	0
Cicatricosisporites venustus Deák 1963	2	0.290	1	0.205
Cicatricosisporites spp.	13	1.908	6	1.230
Cingutriletes sp.	1	0.147	1	0.205
Contignisporites spp.	1	0.147	0	0
Crybelosporites sp.	0	0	1	0.205
Deltoidospora australis (Couper 1953) Srivastava 1975	4	0.587	13	2.664
Deltoidospora minor (Couper 1953) Pocock 1970	8	1.174	27	5.533
Deltoidospora sp.	4	0.587	8	1.640
Densoisporites velatus Weyland & Krieger 1953	1	0.147	1	0.205
Dictyophyllidites harrisii Couper 1958	2	0.290	1	0.205
Echinatisporis sp.	1	0.147	0	0
Gleicheniidites senonicus Ross 1949	0	0	4	0.819
Laevigatosporites sp.	0	0	7	1.434
Leptolepidites sp.	0	0	1	0.205
Patellasporites tavaredensis Groot & Groot 1962	1	0.147	0	0
Retitriletes sp.	0	0	1	0.205
Stereisporites sp.	0	0	1	0.205
Taurucosporites segmentatus Stover 1962	1	0.147	0	0
Trachysporites sp.	1	0.147	0	0
Triporoletes reticulatus (Pocock 1962) Playford 1971	1	0.147	1	0.205
Todisporites major Couper 1958	1	0.147	0	0
Pollen grains (gymnosperms)				
Alisporites bilateralis Rouse 1959	5	0.734	8	1.640
Alisporites spp.	20	2.937	12	2.460
Araucariacites australis Cookson 1947	12	1.762	25	5.123
Callialasporites dampieri Dev 1961	1	0.147	0	0
Cedripites sp.	1	0.147	0	0
Classopollis classoides Pflug 1953 emend. Pocock & Jansonius 1961	213	31.277	46	9.426
Classopollis spp.	58	8.517	9	1.844
Cycadopites spp.	8	1.174	2	0.410
Eucommiidites minor Groot & Penny 1960	4	0.587	2	0.410
Exesipollenites tumulus Balme 1957	6	0.881	3	0.615
Ginkgocycadophytus nitididus (Balme 1957) de Jersey 1962	1	0.147	3	0.615
Inaperturopollenites dubius (Potonié & Venitz 1932) Thompson & Pflug 1953	205	30.102	249	51.024
Inaperturopollenites spp.	21	3.084	9	1.844
Monosulcites chaloneri Brenner 1963	22	3.230	8	1.640
Monosulcites sp.	4	0.587	3	0.615
Pinuspollenites sp.	2	0.290	2	0.410
Podocarpidites sp.	0	0	2	0.410
Spheripollenites sp.	12	1.762	5	1.024
Vitreisporites pallidus (Reissinger 1950) Nilsson 1958	2	0.300	1	0.205
Undetermined bisaccate pollen grains	1	0.147	6	1.230
Pollen grains (angiosperms)				
Afropollis sp.	2	0.300	1	0.205
Clavatipollenites hughesii Couper 1958	2	0.300	3	0.615
Clavatipollenites minutus Brenner 1963	5	0.734	1	0.205
Clavatipollenites sp. (trichomosulcate)	4	0.587	0	0
Clavatipollenites spp.	5	0.734	4	0.819
Liliacidites dividus (Pierce 1961) Brenner 1963	3	0.440	0	0
Pennipollis peroreticulatus Brenner 1963	1	0.147	1	0.205
Tricolpites sp.	1	0.147	0	0
Undetermined angiospermous pollen grains	6	0.881	1	0.205
TOTAL miospores	681	100	488	100

The area could have been covered by mixed conifer forests of Cupressaceae and Cheirolepidiaceae that grew near the sea. Their understory was integrated by pteridophytes, cycads and/or Bennettitales. Ponds and swampy areas were mainly occupied by vascular cryptogams and early angiosperms, which could have aquatic habits. The predominance of *Classopollis* and the lower amount of spores observed in the Peñosas-Cóbreces sample could be related to a drier period. The more humid conditions of Sop-Peñosas are indicated by the higher percentages of *I. dubius* and *Deltoidospora* spp. as well as those of *Laevigatosporites* sp., *Alisporites* spp. and *Araucaricites australis*. Considering their composition, the assemblages are similar to those from the Upper Aptian–Lower Albian sediments of the Oliete sub-basin (Iberian Ranges) (Peyrot et al., 2007a, 2007b).

6 Plant Cuticles

Najarro et al. (2009) reported abundant plant cuticles in the amber-bearing beds of El Soplao outcrop, sometimes as levels up to 10 cm thick. This plant assemblage comprises female cones of the genus *Alvinia*, leafy axes of *Brachyphyllum*-type, *Nehvizdya* sp. (and its reproductive organs classified into the genus *Nehvizdyella*), *Pseudotorellia* sp., and mainly *Frenelopsis* and *Arctopitys* (cited as *Mirovia* in that paper, but see Nosova & Wcisło-Luraniec, 2007).

Up to four-time branched shoots of the cheirolepidiaceous conifer *Frenelopsis* have been collected during the last excavation in July 2009 (Fig. 3.5 and 3.6), due to the large area exposed in the prospect hole excavated. The shoots show lateral branches with a single branch per node, a branching pattern similar to that described and discussed by Daviero et al. (2001). These new records are of taphonomic and paleoenvironmental relevance. From the taphonomic point of view, the stiff, articulated leafy internodes of *Frenelopsis* were probably very brittle and fragmented when transport occurred (Gomez et al., 2001, 2002; Riera et al., 2010). At least for some of the plants of the insect-bearing amber assemblage of El Soplao, such an organization suggests a parautochthonous deposition. The representatives of *Frenelopsis* occupied habitats from freshwater wetlands to saline, coastal or estuarine marshes (e.g. Gomez et al., 2001, 2002; Mendes et al., 2010). Such a wide range of habitats suggests possible mangrove-like ecology for the *Frenelopsis* of El Soplao. This paleoecological inference is also supported by the sedimentological context and the occurrence of marine or brackish-water invertebrates in the sediment and on amber surfaces.

7 Charcoal and Charcoalified Plant Fibers

The first record of charcoalified (=fusainized) plant remains indicating paleofires is from the Silurian from Ludford Lane in the Welsh Borders in England (Glasspool et al., 2004). Scott (2000) provided a general view of the Pre-Quaternary history of fire based on charcoalified plant remains, which are especially important in sediments from the latest Jurassic and Early Cretaceous. Charcoalified plant remains are moderately common in a wide variety of facies, and some notable concentrations of considerable paleobotanical and paleoecological value can occur locally (Nichols et al., 2000).

In Spanish outcrops, amber and charcoal are very scarce except for a few levels in which both appear abundantly. This is the case of all the main outcrops for which this aspect has been explored: Peñacerrada (Suárez-Ruiz, 2003 and López del Valle, per. obs., 2008), La Hoya, San Just (Peñalver et al., 2007, 2008) and El Soplao. In these outcrops there are abundant cuboidal pieces of charcoal (=fusinite) of a few centimeters long (Fig. 7.2), and they are easily recognized with the naked eye even in the field by its silky luster, brittleness and friability. In addition, charcoal pieces are fibrous, black and opaque.

Features of the charcoal associated with amber in El Soplao outcrop using SEM are the undeformed structure and fabric of the tissue with open cell lumina, pits and homogenization of the cell walls (Fig. 7.3–7.5); see Sander and Gee (1990) and Scott (2000, 2010) for general description of charcoal. All of these features revealed by SEM examination are particularly characteristic of a pyrolysis origin. The most important feature is that different layers of the cell wall and adjacent cell walls cannot be distinguished from one to another due to the homogenization during burning. This homogenization of the wall takes place above 300ºC and the resulting charcoal is highly resistant to microbiological or chemical degradation during sedimentation and diagenesis (Cope and Chaloner, 1980). In San Just and El Soplao outcrops charcoal pieces with the cell lumina diagenetically filled with framboidal pyrite are found frequently (Fig. 7.6).

The levels of concentration of amber and charcoal in Spanish outcrops, including El Soplao, reveal paleofires in the resinous forests. Grimaldi et al. (2000) reported wood, insect remains and flowers, all charcoalified, and fire-damaged amber from the Upper Cretaceous (Turonian) of New Jersey, and Jarzembowski et al. (2008) reported a single piece of amber with similar features from the Lower Cretaceous of the Isle of Wight. Brasier et al. (2009) reported abundant examples of amber associated with charcoalified wood from the Early Cretaceous (140 Ma) amber deposit in Hastings (Sussex).

In addition to the frequent presence of charcoal associated with the amber in the same beds, a few amber pieces from El Soplao contain charcoalified plant fibers that appear dispersed inside the amber (Fig. 7.1). It is the first time in the fossil record that charcoalified fibers as bioinclusions have been reported. These fibers are small (around 0.7 mm long) and can be recognized as charcoalified fibers due to both their opaque black color and silky luster. This appearance is not due to the fossildiagenetic process because they contrast to other plant fibers in the same amber pieces that have the common translucent clear brown color without silky luster. These small charcoalified plant fibers became included in resin during paleofires moved by convective currents or, after paleofires, transported by the wind to the exposed resin from the soil of burned areas. Scott et al. (2000) reported how abundant finer charcoal material was transported by wind from a charred area of the Frensham Common Country Park (England) several days

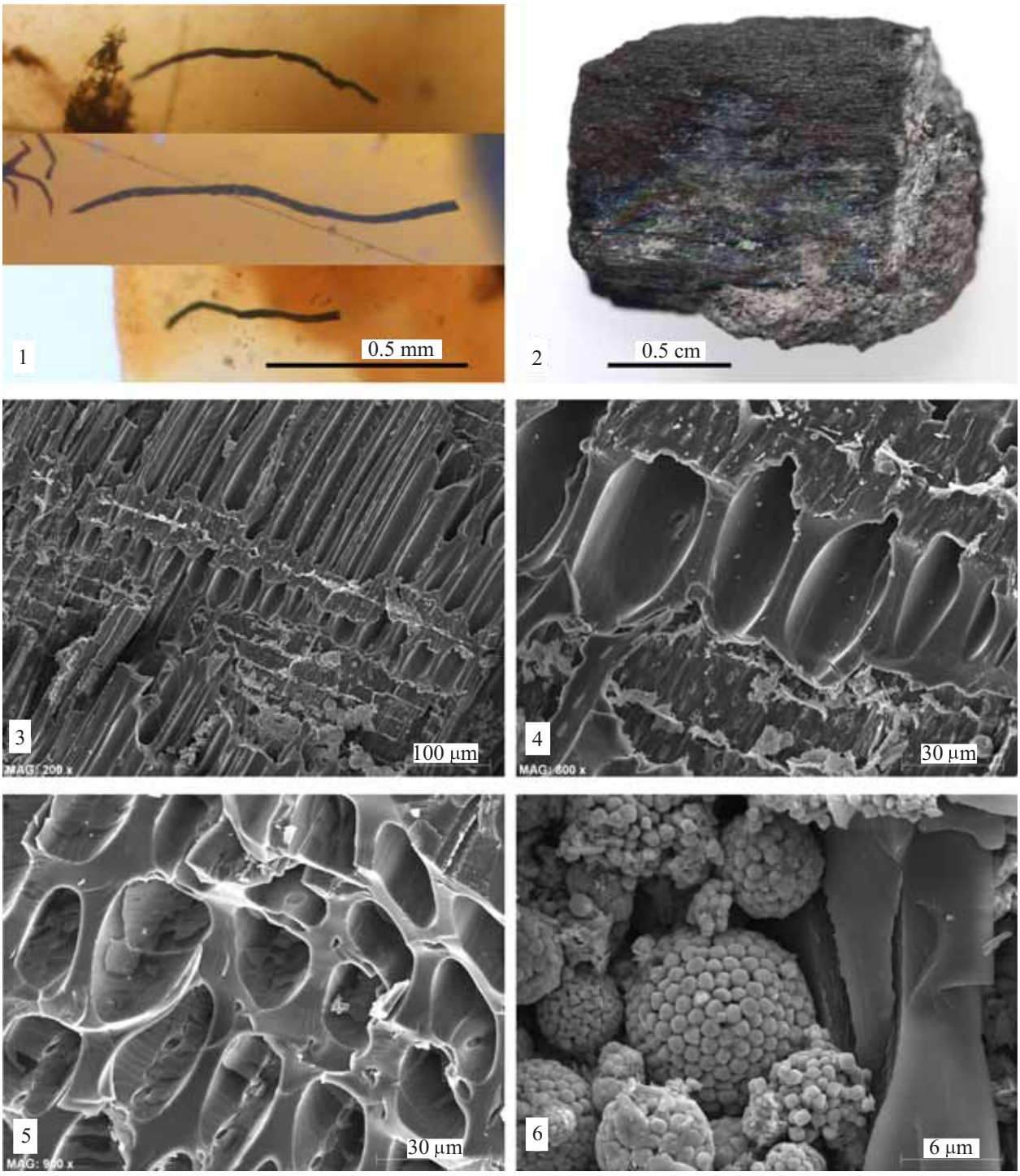


Fig. 7. Fossil carbonized woody tissues (charcoals) from El Soplao outcrop.
1: Three charcoalified plant fibers from the same small amber piece containing numerous of these remains (at the same scale); 2: cuboidal piece of charcoal; 3–5: scanning electron micrographs of charcoals show both pits and cell-wall homogenization in epidermis and peripheral tissues (micrograph 4 is a detail of 3); 6: framboidal pyrite partially filling the cell lumina (micrographs 3–6 are from microsamples of the piece figured in picture 2).

after a wildfire.

The kauri forests (Araucariaceae) of New Zealand most likely are the best extant correlate to the Cretaceous resiniferous forests, except, perhaps, for the fact that the kauri forests do not have a fire ecology (Daniel J. Bickel, pers. comm., 2010). As it has been observed by us in the kauri forests, very large amounts of organic material occur due to the floor accumulation of litter, including resin pieces; Silvester and Orchard (1999) indicated that litter around a large kauri tree may reach 2 m or more in depth, with a mean residence time of 9–78 years due to a slow

decomposition rate. Although resin burns easily, forest fires only affect the litter superficially, except for ground fires (Scott, 2000). Thus the main part of the accumulated resin usually remains intact. Scott et al. (2000) reported a surface fire in the Frensham Common Country Park that charred only a few millimeters of the organic litter, so the pine crown was practically not affected by the fire. As indicated by Grimaldi et al. (2000) and Martínez-Delclòs et al. (2004), forest fires traumatically induced copious production of resin and they might have been an important factor in the genesis of amber deposits. From this respect, Brasier et al. (2009) reported charcoalified conifer wood from Hastings deposit with cell lumina filled with resin after the paleofire. However, we consider that the joined occurrences of large accumulations of amber and charcoal in Spanish outcrops, and abundant plant cuticles as well, were mainly the consequence of an intensive erosion of the litter in burnt forests, possibly including mass wasting; at this respect, Scott & Stea (2002) reported evidences of post-fire soil erosion in Cretaceous charcoal horizons of Nova Scotia. As summarized by Nichols et al. (2000) from different sources, the removal of vegetation by modern fires can increase erosion rates by weathering and during rainstorms by up to 30 times compared with the sink of pre-fire levels, and single wildfire events may be recognizable as responsible for individual depositional units, for example on alluvial fans.

Nichols et al. (2000) conducted actualistic experiments and concluded that charcoal is an unusual sedimentary material because most fresh material floats, but after prolonged immersion becomes waterlogged and sinks, mainly the small pieces. After the study of an area of heathland in SW England burned by an uncontrolled fire, Blackford (2000) concluded that large particles are not transported long distances and thus are indicative of local fires. The great abundances of centimeter-sized charcoal in amber-bearing beds of San Just and El Soplao outcrops suggest that paleofires in these cases were local or occurred close to the area of deposition. In the scenario we propose, intensive erosion by rivers and storm floods of a burned resinous forest area located close to the deltaic environments of deposition was promoted by the loss of vegetation, and resin plus charcoalified wood were transported together through water to coastal environments.

Another complementary factor that could contribute to the great amber accumulation in El Soplao outcrop was proposed by Najarro et al. (2009) based on sedimentological data: floods during rainstorms eroded and removed the resin and plant remains from the soils of coast-fringing forests. Pieces of resin and wood mixed with mud and sand then were transported by density flows to the coastal and interdistributary bays. Surely, more than one of these three factors might have occurred.

We can assume that wildfires had a great impact on environments and most likely they occurred mainly during the warm, drought season; lightning strike is the most important reported cause of naturally ignited fires today (Cope and Chaloner, 1980; Scott, 2010) and it was probably the same during the Cretaceous. Moreover, levels of atmospheric oxygen during the Cretaceous were among the highest during the Phanerozoic, close to 30% (vs. 20% today), leading to a much higher prevalence of fires (Robinson, 1989). Secondary evidence of the environmental impacts of wildfires can be obtained from plant and insect fossil records. The tree fern *Weichselia reticulata* has been recorded in some adjacent beds to the Spanish amber outcrops and this taxon can be related to environments disturbed by both floods and fires according to Coiffard et al. (2007) and Scott et al. (2000). More recently Ortega-Blanco et al. (2008) described a new species of anaxyelid woodwasp, *Eosyntexis parva*, from Peñacerrada I amber closely related to the extant anaxyelid taxa that lay eggs in burnt conifer trees shortly after the wildfires.

8 Marine or Brackish-water Invertebrates on Amber Surfaces

El Soplao amber deposit in some levels contains internal marcasite moulds of marine or brackish-water mollusks, and oyster shells that preserve the original calcium carbonate biomineralization. In addition, for the first time in the fossil record we report findings of large amber pieces that show their surfaces colonized by both serpulid worm tubes (Annelida: Polychaeta) (Fig. 8.1 and 8.2) and encrusting bryozoan colonies (Bryozoa: Cheilostomata) (Fig. 8.3); barnacles encrusting Baltic amber surfaces have been reported, but they are recent barnacles (see Grimaldi, 1996). Amber pieces with their entire surface colonized, or only with one side colonized, have been found.

Serpulid worm tubes exhibit four modes of fossilization that sometimes occur in the same amber piece, but in different parts: (1) as limonitic impressions of the tubes (Fig. 8.1); (2) as internal marcasite moulds (Fig. 8.2); (3) as amber tubes (internal fillings with resin during first fossildiagenetic phases); and (4) as original carbonate remains (Fig. 8.3). Serpulid tube remains are several millimeters long and internal tube fillings are approximately 0.35 mm diameter.

Bryozoan colonies left marks of the zooid exoskeletons on the amber surface and when original calcium carbonate remains are preserved (Fig. 8.3) they easily fade away during the washing of the pieces. Bryozoan colonies are multiserial and belong to the Order Cheilostomata; that group produces mineralized exoskeletons and form single-layered sheets that encrust over surfaces. Box-shaped, rectangular zooids are 0.34 × 0.29 mm in size.

Completeness of these large pieces suggests that they were constituted by polymerized resin when serpulids and bryozoans developed, not fossil resin from eroded strata (reworking process). Resin is comparatively less fragile than amber or copal and, in consequence, more commonly keeps its integrity during marine transport. In any case, this deposit contained a mixture of resin pieces from the litter, and fresh resin pieces directly transported from the trees, together with reworked resin pieces that remained a certain time in saline water. The presence of encrusting bryozoan colonies on the amber surfaces is not surprising because this type of organism is better adapted to shallow, high energy environments. In conclusion, this exceptional record indicates a littoral to coastal marsh

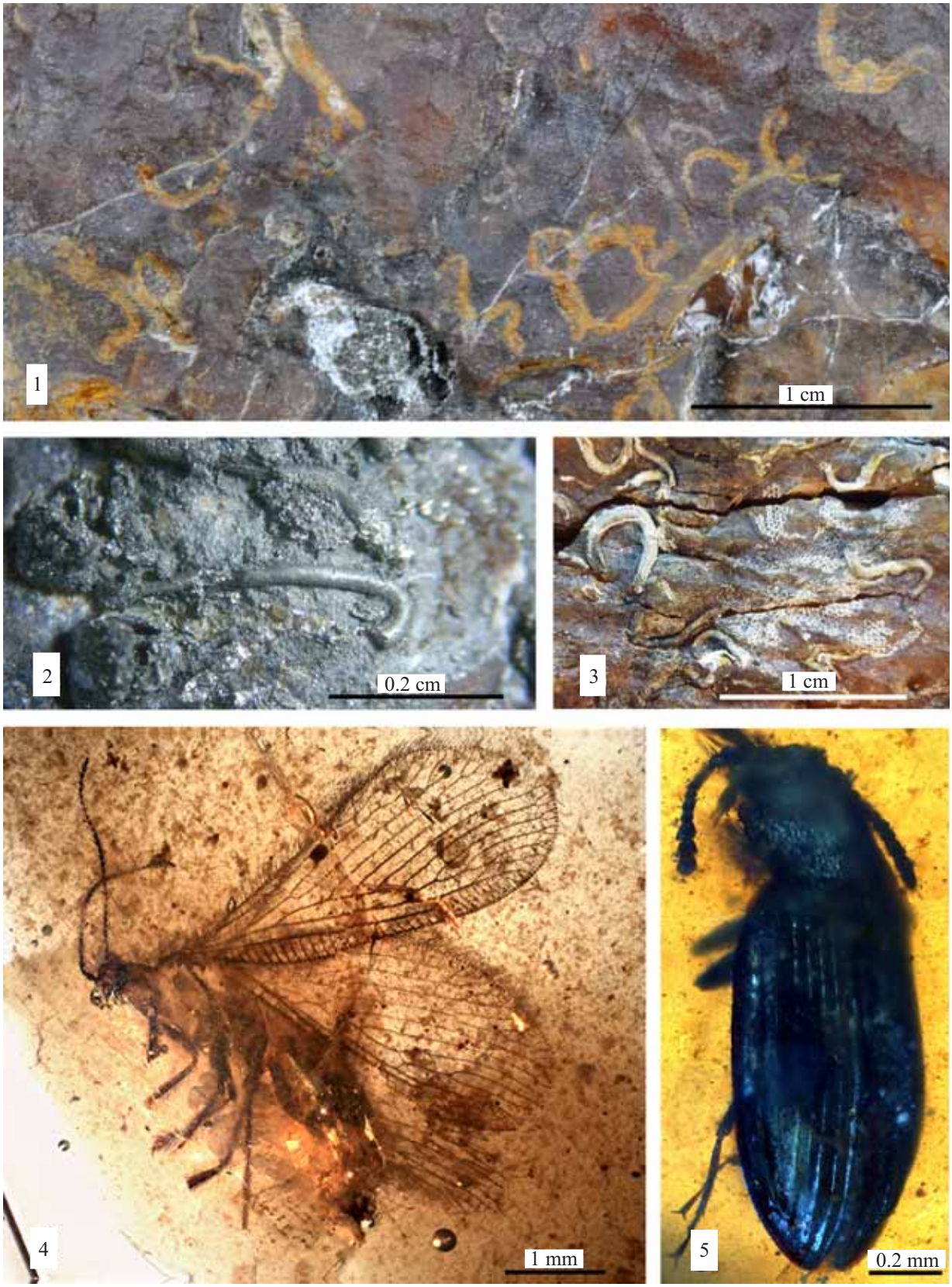


Fig. 8. Marine or brackish-water invertebrates on the surfaces of El Soplao amber and insects as bioinclusions.
1: Detail of the serpulids preserved as limonitic impressions on the entire kidney-shaped amber piece 12 × 10 × 5 cm in size; 2: two serpulid worm tubes preserved as marcasite internal mould of the same amber piece; 3: bryozoan colony and several serpulids preserved as carbonate fossils on the surface of a large amber piece; 4: virtually complete specimen of the family Berothidae (Neuroptera); 5: specimen of Cucujoidea (Coleoptera). Photos 4 and 5 were made with integrated consecutive pictures taken at successive focal planes.

environment of deposition for El Soplao outcrop.

9 New Data on Insect Bioinclusions

Najarro et al. (2009) reported a high abundance of arthropod specimens embedded in the Early Cretaceous amber of El Soplao outcrop, and explained it as a consequence of the unusual concentration of amber pieces indicative of resin flows (drops, crusts and runnels) in this deposit. A significant percentage of amber pieces of this type contains numerous bioinclusions because the original resin was exposed to the atmosphere, was less viscous (it was more easily penetrated by insects), and successive flows encapsulated the trapped insects (Martínez-Delclòs et al., 2004).

Recent paleontological excavations have provided new bioinclusions of significant paleoecological and taxonomical value. To date, El Soplao amber has provided more than 200 bioinclusions, including fungi, plants, and diverse arthropods. Among them, only systematic studies on insects have been already started. The insect inclusions found belong to 11 recognized orders: Blattaria, Isoptera, Psocoptera, Thysanoptera, Raphidioptera, Neuroptera, Hemiptera, Coleoptera, Trichoptera, Hymenoptera, and Diptera; last two groups are the most abundant.

Neuropterid fauna from El Soplao amber is currently being studied. It is composed so far of Neuroptera and Raphidioptera, including the new genus and species of mesoraphidiid described by Pérez-de la Fuente et al. (2010). Neuropterans are represented by two specimens of dustywings (Coniopterygidae) and two beaded lacewings (Berothidae), one of them very complete and interpreted as a new morphotype (Fig. 8.4). Surely, the most outstanding finding is a tentative green lacewing larva (Chrysopidae), which, if confirmed, would be the oldest representative of the family in amber and one of the very few fossil chrysopid larvae ever reported. Its morphology, to be described and discussed elsewhere, is similar to those of the extant trash-carrying chrysopid larvae.

Coleopterans from El Soplao amber are represented only by members of the suborder Polyphaga, and all of them are up to now interpreted as herbivorous or saproxylic forms, most probably living under the bark of the trees. As in other Lower Cretaceous outcrops of surrounding areas in Spain and France, the most abundant forms of beetles from El Soplao belong to superfamilies Elateroidea and Cucujoidea (Fig. 8.5), but there are also present forms of Curculionoidea (?Attelabidae, ?Nemonychidae) and possibly a member of Dascilloidea. The presence of two specimens of Curculionoidea in such small collection of beetles (approximately 10 specimens) is of paleoecological relevance, because this group of beetles in extant ecosystems is closely related to hard parts of trees, in which larval stages developed, and the action damaging trees has also been pointed to as one of the possible causes for the increase in resin-production in trees during the Early Cretaceous and its subsequent record as fossil resins.

Although the hymenopteran assemblage of El Soplao is scarce, it is providing interesting data. It is composed of parasitoid wasps of several superfamilies as Ceraphronoidea (parasitoids of numerous taxa, hyperparasitoids sometimes), Platygastroidea (insect and spider egg parasitoids), Evanioidea (cockroach egg consumers during larval stage), Ichneumonoidea (commonly hyperparasitoids) and Mymarommatoidea (tiny egg parasitoids). Although ceraphronoids are currently under study, a first approximation allows us to recognize members of a recently described new family of Ceraphronoidea (Ortega-Blanco et al., 2010b). In Spanish amber, Ceraphronoids were only detected in the Peñacerrada amber until date; venation and some antennae aspects of the El Soplao morphotype indicate that it belongs to the same genus that is present in Peñacerrada amber. Platygastroids are the most common hymenopteran insects in El Soplao amber, as in all other Spanish ambers, and the study of this group is in progress. Apparently platygastroids belong to a new species with large, 14-articled antennae. A new parasitoid wasp species of the genus *Archaeromma* (Mymarommatoidea) has been recorded in El Soplao, as it was in Peñacerrada I. Recording the same insect species supports the hypothesis that the age of these ambers was equivalent or at least very close, and suggests that both outcrops had similar paleoecological characteristics.

Dipterans from El Soplao amber are represented by Brachycera and Nematocera forms. One specimen of *Litoleptis* sp. (Spaniidae) has been identified within the Brachycera, similar to one specimen described from San Just amber (Arillo et al., 2009). Other dipteran families present include Hybotidae (Brachycera), as well as Cecidomyiidae and Psychodoidea. The current paleodiversity of biting midges (Ceratopogonidae) has been evaluated, leading to the discovery of five species, including three new species (Najarro et al., 2009). The new species belong to the genera *Archiaustroconops*, Szadziewski, 1996, *Atriculicoides* Remm, 1976, and *Lebanoculicoides* Szadziewski, 1996. All these ancient biting midges would have shown a hematophagous diet which is considered plesiotypic within the family (Borkent, 1995).

10 Conclusions

We present herein data that suggest that amber pieces from El Soplao have at least two botanical sources. Part of these data strongly supports a source related to Cheirolepidiaceae and also suggests a molecular relationship of *Frenelopsis* with extant Cupressaceae. This relationship is based on the chemotaxonomic comparison of biological diterpenes found in amber and plant megafossils and extant Cupressaceae.

The taphonomic significance of wildfires in the origin of the Cretaceous amber accumulations has received little attention and has been clearly underestimated. The potential presence of charcoal, fire-damaged amber pieces and charcoalified plant fibers embedded inside the amber must be considered when studying the origin of the Cretaceous amber deposits. In fact, the occurrence of large accumulations of amber and charcoal in Spanish outcrops were consequence of intensive erosion of the litter in burnt forests, possibly including mass wasting. This scenario has been well documented in the case of the El Soplao

deposit, but similar studies on other Spanish amber deposits should be conducted.

The new data on the biological inclusions from El Soplao amber show a highly diversified entomofauna, mainly represented by dipterans and hymenopterans, with the presence of very specialized groups such as chrysopids or weevils, which may help to better understand the early evolution of some insect groups.

The data previously published and new data herein provided suggest a taphonomic history for the El Soplao amber that may have run approximately as follows: resin was exuded by conifers (perhaps by two different conifers, including Cheirolepidiaceae) closely to the deltaic environments of deposition. Conifer forests were well-present in the region, with understory integrated by pteridophytes, cycads and/or Bennettitales; ponds and swampy areas were mainly occupied by vascular cryptogams and early angiosperms, which could have aquatic habits. A diversified insect fauna, mainly represented by hymenopterans and dipterans, developed around the conifer trees and was abundantly embedded in resin. Coleopterans, which probably lived under the bark or in close contact with the wood of the conifer trees, were abundantly embedded as well. Wildfires in the resinous forests promoted both the resin production and an intensive erosion of the partially burned litter. Resin, fresh leaves, wood and charcoal were shortly transported together through water and accumulated alongside marine or brackish-water mollusks in a restricted tidal channel with low circulation and anoxic bottom-water. The conifer *Frenelopsis*, a potential source of resin as suggested by the biogeochemical analyses, grew close to the deposition area, where articulated branched shoots accumulated (parautochthonous deposition). Resin pieces differed in their biostratinomic histories because some of them remained a certain time in shallow, high energy saline waters where serpulids and bryozoans grew on the resin surfaces, resulting in a mixed assemblage. Low circulation and anoxic bottom-water promoted an early pyritization of the marine mollusks, charcoal and amber surfaces, including the fixed serpulid tubes. The assemblage was lastly buried by siltstones and sandstones. The maximum temperatures suffered by the amber deposit during diagenesis were in the range of 60–70ºC. The inferred low maturity levels were maybe responsible for the good preservation of amber molecular composition and its biological inclusions.

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Anexo I.3

A new Early Cretaceous snakefly (Raphidioptera: Mesoraphidiidae) from El Soplao amber (Spain)

Una nueva mosca serpiente del Cretácico Inferior (Raphidioptera: Mesoraphidiidae) del ámbar de El Soplao (España)

Referencia completa:

Pérez-de la Fuente, R., Nel, A., Peñalver, E. & Delclòs, X. 2010. A new Early Cretaceous snakefly (Raphidioptera: Mesoraphidiidae) from El Soplao amber (Spain). *Annales de la Société entomologique de France* 46(1-2): 108-115.

Resumen:

Un ejemplar virtualmente completo perteneciente a la familia Mesoraphidiidae (Insecta: Raphidioptera) se describe como *Cantabroraphidia marcanoi* **n. gen., n. sp.** El ejemplar fue hallado en ámbar del Albiense Inferior, en un nuevo yacimiento nombrado El Soplao y que se localiza en la Formación Las Peñosas, en el Noroeste de Cantabria (España). El nuevo taxón se ha comparado con todos los fósiles adultos clasificados en la familia mesozoica Mesoraphidiidae. Se proporcionan algunos comentarios taxonómicos, y se propone restaurar el género *Yanoraphidia* Ren 1995 y la combinación *Yanoraphidia gaoi* Ren 1995 stat. rest., provisionalmente clasificado en la familia Mesoraphidiidae.

A new Early Cretaceous snakefly (Raphidioptera: Mesoraphidiidae) from El Soplao amber (Spain)

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Abstract. A virtually complete specimen of the family Mesoraphidiidae (Insecta: Raphidioptera) is described as *Cantabroraphidia marcanoi* **n. gen., n. sp.** It was found in early Albian amber from a new deposit named El Soplao within the Las Peñosas Fm. in northwestern Cantabria (Spain). It has been compared to all adult fossils placed in the Mesozoic family Mesoraphidiidae. Some taxonomical comments are provided, and we propose to restore the genus *Yanoraphidia* Ren 1995 and the combination *Yanoraphidia gaoi* Ren 1995 stat. rest., provisionally retained in the family Mesoraphidiidae.

Résumé. Un nouveau Mesoraphidiidae de l'ambre crétacé inférieur de El Soplao (Espagne) (Raphidioptera). Un spécimen presque complet de Mesoraphidiidae (Insecta: Raphidioptera) est décrit sous le nom de *Cantabroraphidia marcanoi* **n. gen., n. sp.** Il a été découvert dans un ambre Albien inférieur d'un nouveau gisement nommé El Soplao dans la Formation Las Peñosas, dans le nord-ouest de la Cantabrie (Espagne). Il est comparé à tous les adultes fossiles placés dans la famille mésozoïque des Mesoraphidiidae. Nous proposons de restaurer le genre *Yanoraphidia* Ren 1995 et la combinaison *Yanoraphidia gaoi* Ren 1995 stat. rest., provisoirement maintenu dans la famille Mesoraphidiidae.

Keywords: Raphidioptera; Mesoraphidiidae; Cretaceous amber; Spain.

Snakeflies (Insecta: Raphidioptera) are holometabolous predatory insects recognised by their elongate prothorax, which gives them their "snake" shape, the characteristic wing venation, and the existence of a long ovipositor in females. Although the first evidence of snakeflies is from the Early Jurassic, the origin of their lineage starts earlier, possibly at the end of the Palaeozoic, becoming widespread during the Mesozoic in Laurasia (Grimaldi 2000). Today snakeflies show a relict diversity and a geographically restricted distribution in cold temperate regions of the North Hemisphere exclusively in Northwestern America, the Mediterranean, and Central Asia (Aspöck *et al.* 1991), living in arboreal habitats and needing at least one period of cold to achieve maturity. Nevertheless, Grimaldi & Engel (2005) pointed out that snakeflies had an intertropical/subtropical distribution until the Early Cainozoic. As figure 1 shows, the fossil record of the Jurassic-Cretaceous family Mesoraphidiidae coincides with the warm temperate/paratropical climate belt *sensu* Scotese (2000), which was between 30ºN and 60ºN. The majority of the fossils of this family of raphidiopterans are preserved as compression fossils, and only a few specimens are known as inclusions in amber.

An unusual concentration of Cretaceous aerial amber with abundant bioinclusions has been recently discovered in El Soplao territory, in the Spanish municipality of Rábago in Cantabria (Najarro *et al.* 2009). The bioinclusions found so far are spiders and spider webs, and many insects of the orders Blattaria, Hemiptera, Thysanoptera, Raphidioptera, Neuroptera, Coleoptera, Hymenoptera, and Diptera. Here we describe one specimen of the order Raphidioptera, extending the knowledge and the palaeobiogeography of Cretaceous snakeflies. Due to the scarce fossil record of this group, any new findings of its fossil representatives are of particular interest.

Geological setting

The El Soplao outcrop is early Albian in age (Najarro *et al.* 2009) and is included in the same geological context as other north Spanish amber-bearing deposits (see Delclòs *et al.* 2007). El Soplao territory is located at the north-western margin of the Basque-Cantabrian Basin, which developed during the Cretaceous. The

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formation of the Basque-Cantabrian Basin is related to the opening of the Atlantic Ocean and the kinematics between the European and Iberian plates (Malod & Mauffret 1990; Olivet 1996). The amber-bearing deposit of El Soplao is included within the Las Peñosas Fm., in a unit of heterolithic sandstones-siltstones and carbonaceous mudstones deposited in coastal estuarine and delta marine environments (Najarro *et al.* 2009). The amber pieces were collected from a level 0.7 m to 2.5 m thick, of organic-rich clays, associated with abundant plant cuticle remains mainly of the conifer genera *Frenelopsis* (Schenk 1869) emend. Watson 1977 and *Mirovia* Reymanówna 1985 emend. Bose & Manum 1990, and ginkgoalean genera *Nehvizdya* Hluštík 1977 and *Pseudotorellia* Florin 1936 (see Najarro *et al.* 2009).

Material and methods

The specimen was found during stratigraphic fieldwork in 2008 by researchers of the Instituto Geológico y Minero de España (Madrid). Preparation involved the removing of the main part of surrounding amber in order to obtain the best visibility of the fossil, because the amber piece contains abundant debris. The prepared amber was mounted in Epoxy resin (EPO-TEK 301) following the protocol of Corral *et al.* (1999). The fossil was examined, drawn and measured using a binocular Olympus SZX9 stereomicroscope, an inverted Olympus CK40 compound microscope, and a direct Leitz microscope. Photographs were taken using a digital camera attached to an Olympus BX51 microscope. Some images were reconstructed using the computer software Combine Z5 and forewing venation was reconstructed using the two incomplete forewings in the fossil.

Morphological terminology follows that of Aspöck *et al.* (1991).

Systematic palaeontology

Order Raphidioptera Navás 1916

Family Mesoraphidiidae Martynov 1925

Genus *Cantabroraphidia* n. gen.

Type species. *Cantabroraphidia marcanoi* **n. sp.**

Etymology. Named after "Cantabria", the Spanish Autonomic Community where the outcrop is located.

Diagnosis. Minute size (forewing length 5.5 mm). Head more or less quadrangular; three large ocelli present, situated between anterior half of compound eyes; posterior border of head with a distinct collar-like lip; antenna inserted posterior to clypeal-frons suture, slightly basad of anterior tangent of compound eyes; antenna distinctly longer than head; compound eyes large and exophthalmic; coronal suture possibly absent. Pronotum subequal in length to head length, with anterior

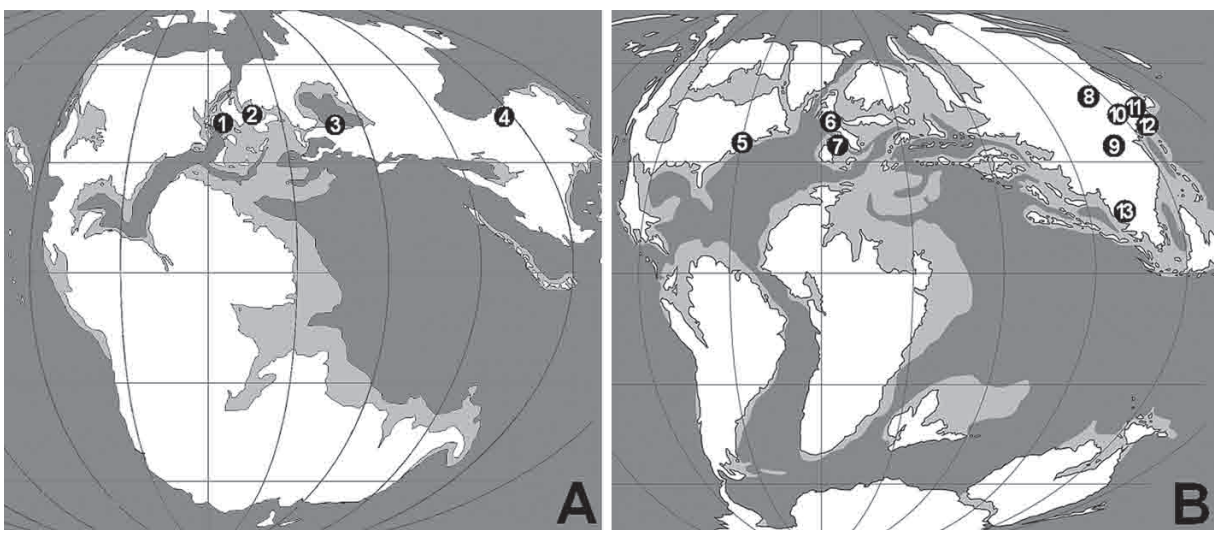

Figure 1
Palaeogeographical distribution of localities with described species of the family Mesoraphidiidae (after Engel 2002, and Jepson & Jarzembowski 2008). **A,** Jurassic Period. **1**, Dorset, England. *Metaraphidia confusa*. **2**, Niedersachsen, Germany. *Metaraphidia vahldieki*. **3**, South Kazakhstan, Kazakhstan. *Mesoraphidia elongata*, *M. grandis*, *M. inaequalis*, *M. parvula*, *M. pterostigmalis*, *M. similis*; *Proraphidia turkestanica*. **4**, Dundgobi Aimag, Mongolia. *Mesoraphidia gobiensis*. **B,** Cretaceous Period. **5**, New Jersey, USA. *Mesoraphidia luzzii*. **6**, Southern England. *Mesoraphidia durlstonensis*, *M. mitchelli*, *M. purbeckensis*, *M. websteri* (Dorset County). *Proraphidia hopkinsi* (Surrey County). **7**, Spain. *Cantabroraphidia marcanoi* **n. gen., n. sp**. (Albian of the Cantabria, Northern Spain). *Proraphidia gomezi* (Early Barremian of the Lleida Province, Northeastern Spain). **8**, Buryat Republic, Russia. *Baisoraphidia glossopteron*, *B. orientalis*; *Siboptera eurydictyon*, *S. medialis*. **9**, Gansu, China. *Sinoraphidia viridis*. **10**, Liaoning, China. *Huaxiaraphidia shandongensis*, *H. sinensis*; *Kezuoraphidia kezuoensis*; *Mesoraphidia amoena*, *M. furcivenata*, *M. glossophylla*, *M. heteroneura*, *M. longistigmosa*, *M. myrioneura*, *M. obliquivenatica*, *M. polyphlebia*, *M. shangyuanensis*, *M. sinica*; *Siboptera fornicata*; *Xuraphidia liaoxiensis*; *Yanoraphidia gaoi* **stat. rest. 11**, Jilin, China. *Jilinoraphidia dalaziensis*. **12**, South Korea. *Mesoraphidia koreenensis*, *M. phantasma*. **13**, Kachin, Myanmar. *Nanoraphidia electroburmica*. (Redrawn from Blakey 2008).

half narrowed dorsoventrally relative to posterior half (i.e., with slight downward curve in lateral view). Forewing with costal area relatively broad, at widest point costal field as broad as pterostigma; pterostigma elongate, without cross-veins; Sc terminating into C in distal two-third of wing length; two medial cells posterior to Mp; first cua-cup cross-vein strongly basad of Mp-Cua separation (at or separated by a few vein widths in other mesoraphidiids, except *Nanoraphidia* Engel 2002). Process at half of the metatibiae in a posterior position; tibiae with apical spines.

Cantabroraphidia marcanoi n. sp. (Figs 2–4)

Material. Holotype specimen ES-07-6, a virtually complete adult of sex unknown, with the wings partially damaged (fig. 4.1). It was found within a mass of transparent amber, collected by M. Najarro and I. Rosales. It is provisionally housed at the Museo Geominero (IGME) in Madrid (Spain). The amber also contains a dipteran adult as a syninclusion (ES-07-7). The sample has abundant debris that makes the study of the specimen difficult.

Diagnosis. As for the genus.

Etymology. The specific epithet is patronymic honouring Mr. Francisco Javier López Marcano ("Consejería de Cultura, Turismo y Deportes", Government of Cantabria) for his efforts and promotion of the study of El Soplao amber.

Age and outcrop. Early Cretaceous (early Albian) in Las Peñosas Fm. Amber-bearing outcrop from El Soplao territory in northwestern Cantabria (near the village of Rábago), Spain (see Najarro *et al.* 2009).

Description. As for the genus with the following additions: Integument dark brown, with maculations on legs (see fig. 2–4.5). Mandible with teeth hardly visible; palps short, not easily visible; compound eye length slightly longer than head posteriad posterior tangent of compound eyes; compound eyes separated by distance nearly 2 times greater than compound eye length; inner margins of compound eyes relatively straight and parallel; 28 antennal segments (fig. 2–4.3), flagellomeres each about as long as wide, with sparse, minute setae (fig. 4.2). All tibiae with apical spines; metatibiae with a process at its midpoint (fig. 4.6). Five tarsal segments, third bilobed (fig. 4.7); claws apparently simple but with a long basal seta and a basal enlargement (fig. 4.8); arolium large. Wing veins brown with strong setae (fig. 4.8), membrane hyaline. Forewing length ca. 5.5 mm, width 1.8 mm; with pterostigma elongate (1.4 mm long) and faintly infumate (fig. 3.1–3.2), situated 0.4 mm (three and half times pterostigmal width) beyond termination of Sc; pterostigma without transverse cross-veins, basally closed by a cross-vein; pterostigma longer than either radial cell; veins meeting wing margins not apically bifurcate; four costal cross-veins (c-sc); single, proximal sc-r cross-vein; two large radial cells present, with two posterior cells immediately behind and progressively decreasing in size; first radial cell nearly as long as second radial cell, with posterior radial branch arising slightly distad its midpoint; two medial cells present; Mp-Cua separation positioned closer to second cua-cup cross-vein than to first; 2A strongly arcuate; jugal lobe not visible. Basal half of a hindwing partially preserved, with only the proximal area of the pterostigma conspicuous (fig. 3.3); costal area distinctly narrower than in forewing; apex of Sc well basal of pterostigma; Mp with two medial cells, the first one smaller and trianguloid; 1ma-mp cross-vein very close to the branching between Rs and Ma; anal area narrow. Thorax, except prothorax, and abdomen largely crushed, but overall length roughly the same as the head plus the prothorax. Anterior part of dorsal side of prothorax with a band of small spines.

Discussion

Engel (2002) proposed a commented list of fossil Raphidioptera, including several nomenclatural changes. A few taxa have been described later (for the latest summaries see Engel & Ren 2008 and Jepson &

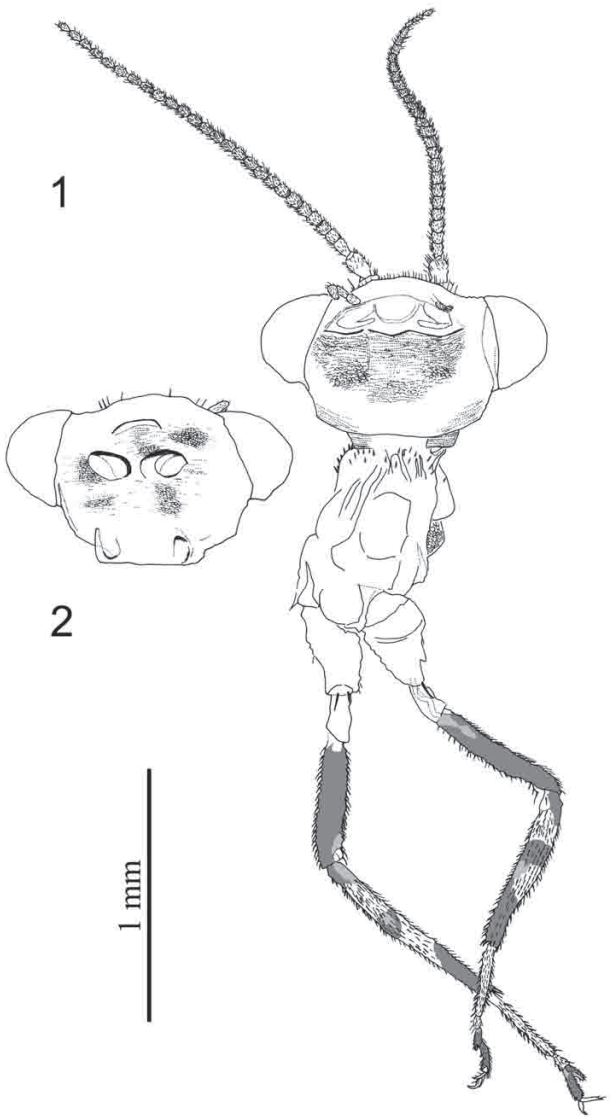

Figure 2
Camera lucida drawing of *Cantabroraphidia marcanoi* **n. gen., n. sp.**; holotype ES-07-6. **1)** Head, pronotum and fore legs in ventral view and, **2)** Detail of head in dorsal view. Note the colour pattern preserved in legs.

Jarzembowski 2008). Two localities indicated as Jurassic-Cretaceous by Engel (2002), the Jiuquan Basin (Gansu, China) and Baissa (Buryat, Russia), have been previously considered to be Cretaceous (Hong 1988; Zherikhin & Gratshev 2004) (fig. 1). Engel (2002) noticed that the general classification of the Mesozoic Raphidioptera is far from being satisfactory due to the different families probably being paraphyletic. With the present state of raphidiopteran taxonomy, *Cantabroraphidia marcanoi* **n. gen., n. sp.** can be attributed to Mesoraphidiidae Martynov 1925 rather than to Baissopteridae Martynova 1961 or Alloraphidiidae Carpenter 1967, because of its great similarity in wing venation with mesoraphidiid genera like *Nanoraphidia* Engel 2002. Figure 1 shows the palaeogeographical distribution of the family Mesoraphidiidae during the Jurassic and Cretaceous.

Thirteen genera are currently attributed to the Mesoraphidiidae: *Mesoraphidia* Martynov 1925, *Proraphidia* Martynova 1947, *Sinoraphidia* Hong 1982, *Metaraphidia* Whalley 1985, *Jilinoraphidia* Hong & Chang 1989, *Huaxiaraphidia* Hong 1992, *Xuraphidia* Hong 1992, *Baisoraphidia* Ponomarenko 1993, *Siboptera* Ponomarenko 1993, *Kezuoraphidia* Willmann 1994, *Yanoraphidia* Ren 1995, *Nanoraphidia* Engel 2002 and *Cantabroraphidia* **n. gen.** We have compared *Cantabroraphidia marcanoi* **n. gen., n. sp.** to all the described Mesoraphidiidae, and to the genera *Ororaphidia* Engel & Ren 2008 and *Styporaphidia* Engel & Ren 2008, which are of uncertain position but have a wing venation similar to those of Mesoraphidiidae.

The species of the genus *Metaraphidia* Whalley 1985 have obscured pterostigmata. *Metaraphidia confusa* Whalley 1985 (Lower Jurassic of England) has a forewing length of 14.5 mm and *Metaraphidia vahldieki* Willmann 1994 (Lower Jurassic of Germany) has a forewing 8.5 mm long (Whalley 1985; Willmann 1994). *Ororaphidia* Engel & Ren 2008 (*O. megalocephala* Engel & Ren 2008, Middle Jurassic of China, has a forewing length of 11.4 mm, with wing venation superficially similar to some *Mesoraphidia*), and *Styporaphidia* Engel & Ren 2008 (*S. magia* Engel & Ren 2008, Middle Jurassic of China, with a wing length of 10 mm), have at least one cross-vein in the pterostigma (Engel & Ren 2008). The species of the genus *Proraphidia* Martynova 1947 (*P. turkestanica* Martynova 1947, Upper Jurassic of Kazakhstan, *Proraphidia gomezi* Jepson & Jarzembowski 2008, Lower Cretaceous of Spain, and *Proraphidia hopkinsi* Jepson & Jarzembowski 2008, Lower Cretaceous of England) have wings between 11–13 mm long and very short pterostigmata (Martynova 1947; Jepson & Jarzembowski 2008).

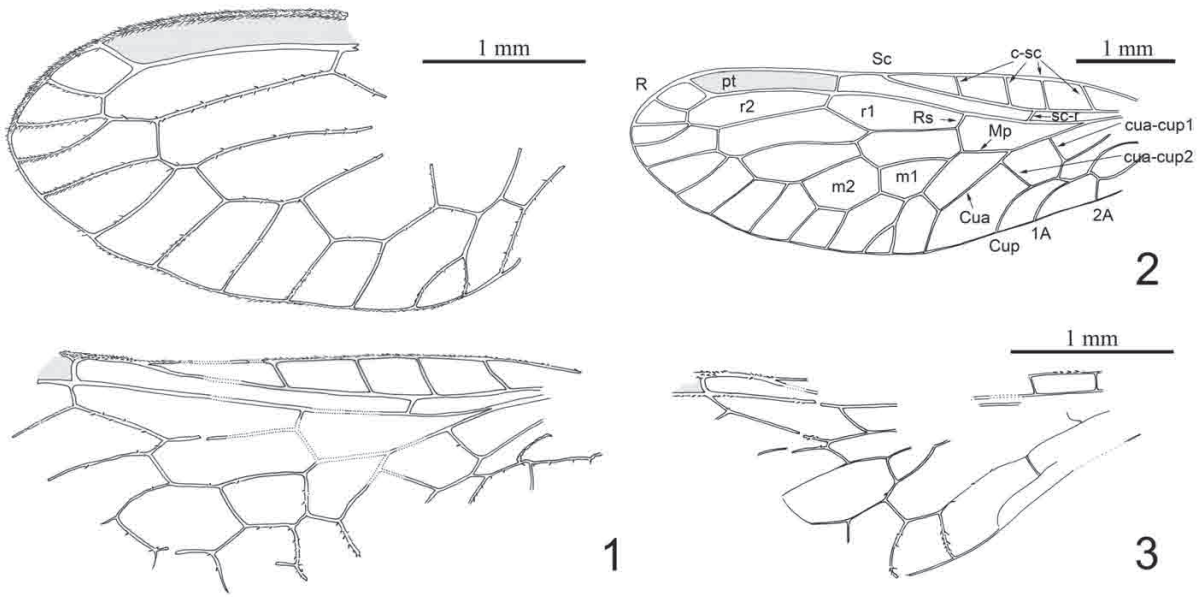

Figure 3
Cantabroraphidia marcanoi **n. gen., n. sp.**; holotype ES-07-6. **1,** Distal and proximal portions preserved of two forewings (*camera lucida* drawings); **2**, Tentative reconstruction of the forewing based on the two preserved portions (some parts appear deformed with respect to the original preserved portions); **3**, Preserved portion of hindwing. 1A/2A = anal veins, c-sc = costal cross-veins, Cua = Cubital anterior vein, Cup = Cubital posterior vein, cua-cup1/cua-cup2 = cubito-anal cross-veins, m1/m2 = medial cells, Mp = Median posterior vein, pt = pterostigma, R = Radial vein, r1/r2 = radial cells, Rs = Radial sector, Sc = Subcostal vein, sc-r = subcostal-radial cross-vein.

The genus *Mesoraphidia* Martynov 1925 comprises of many Jurassic and Cretaceous species, but it is probably not a natural group. The type species *Mesoraphidia grandis* Martynov 1925 (Upper Jurassic of Kazakhstan) has a wing length of 16 mm, a short common stem of Mp and Cua, and a very long marginal cell between R and Rs (Martynov 1925a,b), unlike *Cantabroraphidia* **n. gen.** *Mesoraphidia elongata* Martynov 1925 (Upper Jurassic of Kazakhstan) has a wing 9.5 mm long, and the same differences with *Cantabroraphidia marcanoi* **n. gen., n. sp.** as *M. grandis* Martynov 1925. *Mesoraphidia inaequalis* Martynov 1925 (Upper Jurassic of Kazakhstan) has a wing length of 16 mm. *Mesoraphidia parvula* Martynov 1925 (Upper Jurassic of Kazakhstan) has a wing 5.5 mm long, but its last cross-vein between the anterior branch of Rs and Ma is aligned with that between Ma and Mp, and the stem of Ma is long before it apically divides (Martynov 1925a,b). *Mesoraphidia similis* Martynov 1925 (Upper Jurassic of Kazakhstan) has a wing length of 15 mm (Martynov 1925a,b), and a long marginal cell between R and Rs, unlike *Cantabroraphidia marcanoi* **n. gen., n. sp.** *Mesoraphidia pterostigmalis* Martynova 1947 (Upper Jurassic of Kazakhstan) has a forewing 13 mm long, a short common stem of Mp and Cua, and a very long marginal cell between R and Rs (Martynova 1947), unlike the new species described herein. *Mesoraphidia gobiensis* Ponomarenko 1988 (Upper Jurassic of Mongolia) has wing 8.5 mm long, and a longer marginal cell between R and the anterior branch of Rs (Ponomarenko 1988). The new taxon also differentiates from several species of *Mesoraphidia* described in the Lower Cretaceous of China by Ren (1994, 1995, 1997), previously placed in several genera (see Engel 2002). *Mesoraphidia longistigmosa* (Ren 1994) has a forewing 15 mm long, and a short common stem of Mp and Cua. *Mesoraphidia obliquivenatica* (Ren 1994) and *Mesoraphidia polyphlebia* (Ren 1994) have forewings 16 mm long and similar short common stems of Mp and Cua (Ren 1994; Engel 2002). The same situation occurs for *Mesoraphidia shangyuanensis* (Ren 1994) with a forewing length of 13 mm. *Mesoraphidia gaoi* (Ren 1995) has a forewing 5 mm long, similar to *Cantabroraphidia marcanoi* **n. gen., n. sp.**, but its pterostigma goes up to the apex of R, unlike the new species but also unlike *M. grandis*, the type species of the genus. Ren in Ren *et al.* (1995) described it originally in the genus *Yanoraphidia* Ren 1995, but Engel (2002) transferred it to *Mesoraphidia*. This important difference is clearly visible in the photograph of the holotype and justifies the attribution of *M. gaoi* to a different genus. Thus we propose to restore the genus *Yanoraphidia* and the combination *Yanoraphidia gaoi* Ren 1995 **stat. rest.** The exact position and relationships of this genus, originally described in the Alloraphidiidae and transferred into the Mesoraphidiidae by Engel (2002), remains rather uncertain even if the second solution seems to be the best, at least provisionally. *Mesoraphidia furcivenata* (Ren 1995) has a forewing 10 mm long and a short common stem of Mp and Cua (Ren *et al.* 1995). *Mesoraphidia amoena* Ren 1997 has a forewing 9 mm long, a first radial cell nearly twice as long as second, and a very long marginal cell between R and Rs (Ren 1997). *Mesoraphidia glossophylla* (Ren 1997) has a forewing 19 mm long, a relatively long common stem of Mp and Cua but a long marginal cell between R and Rs (Ren 1997). *Mesoraphidia heteroneura* Ren 1997 has a forewing 10.5 mm long, and a short common stem of Mp and Cua (Ren 1997). *Mesoraphidia myrioneura* (Ren 1997) has a forewing 18 mm long and three radial cells instead of two, like in *Cantabroraphidia marcanoi* **n. gen., n. sp.** *Mesoraphidia sinica* Ren 1997 has a forewing 11 mm long, and a short common stem of Mp and Cua (Ren 1997). *Mesoraphidia koreenensis* Engel, Lim & Baek 2006 (Lower Cretaceous of South Korea) has a wing 7.0 mm long, but its pterostigma is in a much more distal position and it has a longer marginal cell between R and the anterior branch of Rs (Engel *et al.* 2006). *Mesoraphidia phantasma* Engel, Lim & Baek 2006 (Lower Cretaceous of South Korea) has a wing 6.5 mm long, but its Rs emerges in a much more basal position (Engel *et al.* 2006), plus its common stem Mp+Cua is distinctly shorter than in *Cantabroraphidia marcanoi* **n. gen., n. sp.** Recently four new species of the genus *Mesoraphidia* have been described from the Lower Cretaceous of England (Jepson *et al.* 2009). *Mesoraphidia durlstonensis* Jepson, Coram & Jarzembowski 2009 has a forewing 10.6 mm long. *Mesoraphidia purbeckensis* Jepson, Coram & Jarzembowski 2009 has an estimated forewing length of 5.1 mm long and *Mesoraphidia websteri* Jepson, Coram & Jarzembowski 2009 has an estimated hindwing length 5.7 mm, similar in length to the Spanish specimen, but both differ in a long marginal cell between R and Rs. *Mesoraphidia mitchelli* Jepson, Coram & Jarzembowski 2009 has a second radial cell relatively very wide compared to its length and R distal to pterostigmal level straight, unlike *Cantabroraphidia marcanoi* **n. gen., n. sp.** *Mesoraphidia luzzii* Grimaldi 2000 (Upper Cretaceous of USA) has a forewing length of 6.13 mm (Grimaldi 2000), but its basal common stem of Mp and Cua is distinctly shorter than in *Cantabroraphidia marcanoi* **n. gen., n. sp.**

Sinoraphidia Hong 1982 (*S. viridis* Hong 1982, Lower Cretaceous of China) has a forewing about 13.5

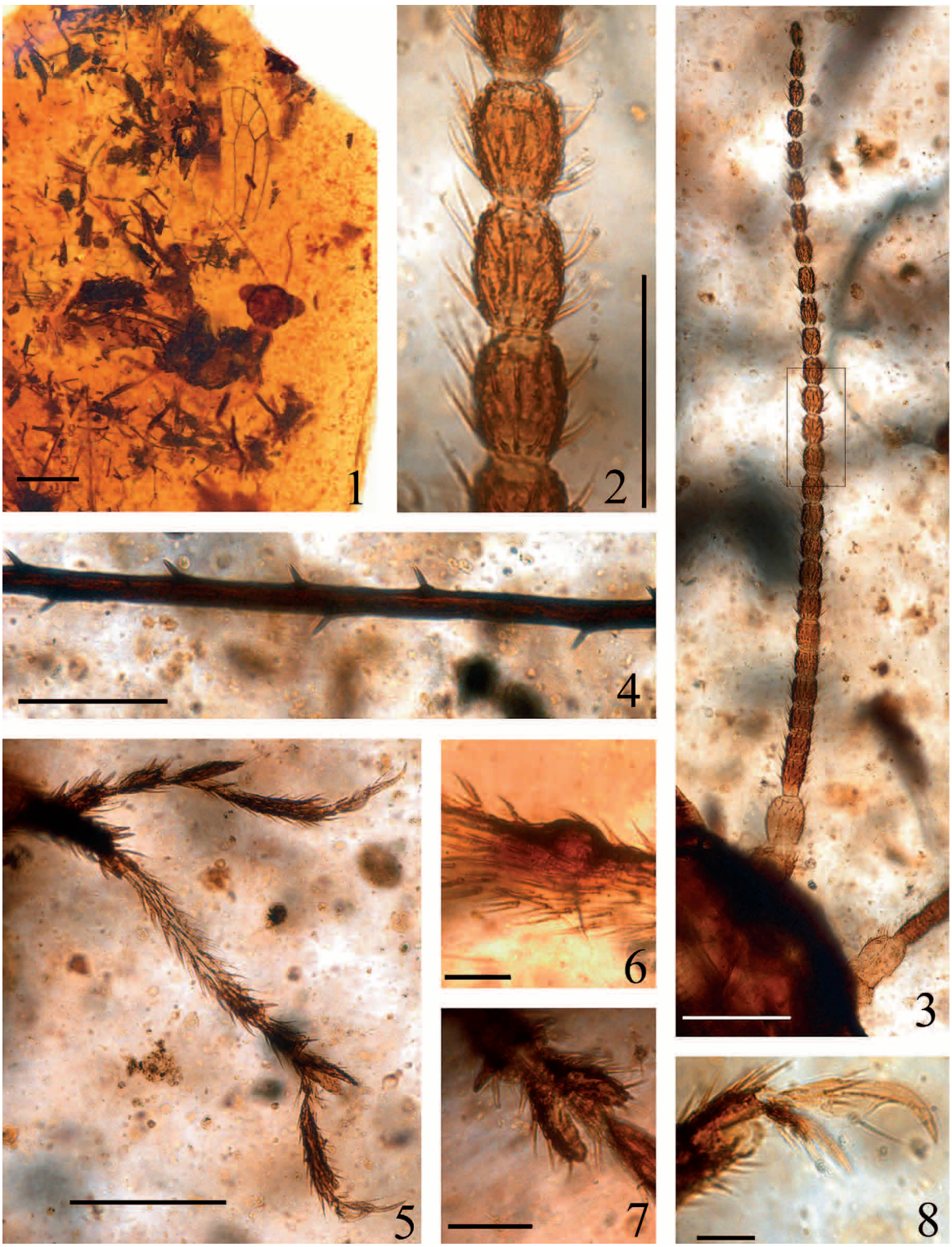

Figure 4
Cantabroraphidia marcanoi **n. gen., n. sp.**; holotype ES-07-6. **1,** dorsal habitus (bar = 1 mm); **2,** detail of flagellomeres (bar = 0.1 mm); **3,** left antenna (bar = 0.2 mm); **4,** detail of setae in forewing vein (bar = 0.1 mm); **5,** meso- (down) and metatarsi (up) (bar = 0.2 mm); **6,** process in metatibiae (bar = 0.025 mm); **7,** bilobed third mesotarsal segment (bar = 0.05 mm); **8,** claw of foreleg (bar = 0.025 mm). Images 3 and 5 are composite, made with consecutive pictures taken at successive focal planes.

mm long, and apparently a short common stem of Mp with Cua (Hong 1992a). *Jilinoraphidia* Hong & Chang 1989 (*Jilinoraphidia dalaziensis* Hong & Chang 1989, Lower Cretaceous of China, wing length 24 mm), has numerous cross-veins between R and costal margin near the apex (Hong & Chang 1989). *Huaxiaraphidia* Hong 1992 (*Huaxiaraphidia sinensis* Hong 1992, Lower Cretaceous of China, wing length 14.0 mm, and *Huaxiaraphidia shandongensis* Hong 1992, same age and locality, wing length 12.0 to 13.5 mm) differs from *Cantabroraphidia* **n. gen.** in the very long marginal cell between R and Rs, plus probably a short stem of Mp and Cua (Hong 1992a). *Xuraphidia* Hong 1992 has a wing length of 10.0 mm and three radial cells (Hong 1992b; Willmann 1994). *Baisoraphidia* Ponomarenko 1993 from the Lower Cretaceous of Russia (*B. glossopteron* Ponomarenko 1993, forewing lengths between 10.5 to 11.0 mm; and *B. orientalis* Ponomarenko 1993, forewing lengths between 9.0 to 10.0 mm) differs from *Cantabroraphidia* **n. gen.** in the short common stem of Mp and Cua (Ponomarenko 1993). *Siboptera* Ponomarenko 1993 differs from *Cantabroraphidia* **n. gen.** in the presence of a cross-vein in the pterostigma (Ponomarenko 1993). Also *Siboptera eurydictyon* Ponomarenko 1993 from the Lower Cretaceous of Russia has forewings between 9.3 and 10.5 mm long, *S. medialis* Ponomarenko 1993 (Lower Cretaceous of Russia) has a forewing 13.5 mm long, and *S. fornicata* Ren 1994 (Lower Cretaceous of China) has a forewing 20 mm long and a long marginal cell between R and the anterior branch of Rs (Ponomarenko 1993; Ren 1994). *Kezuoraphidia* Willmann 1994 has a longer marginal cell between R and the anterior branch of Rs; also, *Kezuoraphidia kezuoensis* (Hong 1992) from the Lower Cretaceous of China has a forewing about 18 mm long (Hong 1992b; Willmann 1994). *Nanoraphidia* Engel 2002 (*N. electroburmica* Engel 2002, Upper Cretaceous of Myanmar), has a very short forewing, 4.26 mm long, and a long common stem of Mp and Cua as for *Cantabroraphidia* **n. gen.**, but it differs from the new taxon due to the presence of only one medial cell posterior to Mp (see Engel 2002).

Conclusions

After comparison of the studied specimen with all the other genera of the family Mesoraphidiidae, we propose the new genus *Cantabroraphidia* and the new species *C. marcanoi* for the first raphidiopteran found in El Soplao amber (Spain). It is distinguished from all the other Mesoraphidiidae by the characteristics of the head and wing size plus forewing venation features.

As with the other known Mesoraphidiidae, *Cantabroraphidia marcanoi* **n. gen., n. sp.** lived within the warm temperate/paratropical climatic belt that prevailed in the Northern Hemisphere during the Cretaceous. Although Raphidioptera are recorded from the Lower Cretaceous of the Southern Hemisphere (Santa Ana do Carirí, Brazil), Mesoraphidiidae seem to have been restricted to the Northern Hemisphere. Nevertheless, conclusions on the distributions of the different Mesozoic snakefly families shall give a much better understanding of the limits and monophyly of these groups.

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Anexo I.4

Synchrotron X-ray imaging of inclusions in amber

Técnicas de imagen con rayos-X sincrotrón para inclusiones en ámbar

Referencia completa:

Soriano, C., Archer, M., Azar, D., Creaser, P., Delclòs, X., Godthelp, H., Hand, S., Jones, A., Nel, A., Néraudeau, D., Ortega-Blanco, J., **Pérez-de la Fuente, R.**, Perrichot, V., Saupe, E., Solórzano-Kraemer, M. & Tafforeau, P. 2010. Synchrotron X-ray imaging of inclusions in amber. *Comptes Rendus Palevol* 9(6-7): 361-368.

Resumen:

A lo largo de estos últimos seis años, se han descubierto y estudiado inclusiones orgánicas preservadas en muestras de ámbar de yacimientos distribuidos mundialmente usando técnicas de imagen basadas en la propagación de contraste de fase con rayos-X sincrotrón, en la European Synchrotron Radiation Facility (ESRF). Se proporciona una breve descripción de las técnicas y protocolos utilizados para la detección y representación virtual no destructiva de las inclusiones en ámbar, así como los últimos resultados de los principales proyectos del ámbar en la ESRF, ilustrándose la creciente utilidad de la microtomografía por contraste de fase con radiación X sincrotrón.

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General palaeontology

Synchrotron X-ray imaging of inclusions in amber

Imagerie par rayonnement X synchrotron d'inclusions dans l'ambre

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ABSTRACT

Over the past six years, organic inclusions preserved in amber samples from outcrops worldwide have been discovered and imaged in 3D using propagation phase contrast based X-ray synchrotron imaging techniques at the European Synchrotron Radiation Facility (ESRF). A brief description of the techniques and protocols used for detecting and 3D non-destructive imaging of amber inclusions is provided. The latest results from the major amber projects in the ESRF are given, illustrating the increasing utility of the imaging capabilities of X-ray synchrotron phase contrast microtomography.

RÉSUMÉ

Au cours des six dernières années, de nombreuses inclusions d'organismes préservés dans des ambres d'origines géographiques diverses ont été imagées en trois dimensions, voire découvertes, grâce à la microtomographie à haute résolution en contraste de phase à rayonnement X synchrotron, à l'Installation Européenne de Rayonnement Synchrotron (ESRF, Grenoble, France). Une brève description des techniques et protocoles utilisés pour la détection et l'imagerie 3D non destructive des inclusions de l'ambre est fournie. Les

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derniers résultats des principaux projets engagés sur l'ambre à l'ESRF présentés ici montrent l'intérêt croissant des possibilités d'imagerie par microtomographie en rayonnements X synchrotron.

1. Introduction

Amber results from the fossilization of various tree resins and is found in sediments dating from the Paleozoic to Holocene. Although the oldest ambers with biological remains (microorganisms) date from the Triassic (Schmidt et al., 2006), macroinclusions have not been found in sediments older than the Lower Cretaceous (c.a. Grimaldi and Engel, 2005; Martínez-Delclòs et al., 2004). Due to the exceptional preservation of organisms in amber, these Lagerstätten often preserve a significant part of the ecosystems in which the amber-producing trees lived. Further, ethological behaviour may be captured (such as evidence of phoresis or parasitism). Various studies have demonstrated that it is possible to obtain information about the soft anatomy of organisms preserved in amber (Grimaldi et al., 1994; Penney et al., 2007; Poinar and Hess, 1982), although most of these techniques led to the destruction of the sample (e.g. Grimaldi et al., 1994).

Amber opacity varies greatly among deposits and between samples from the same outcrop. In some cases, the transparency of the resin is high enough to allow the study of the inclusions by classical optic methods (binocular, electronic and confocal microscopes). However, in other cases, the inclusions may be obscured by amber impurities, white foams (due to presence of microbubbles) or oxidation or hydration processes (Martínez-Delclòs et al., 2004), greatly decreasing access to anatomical data of the animal or plant preserved in the resin. In extreme cases, the amber pieces are completely opaque, making it virtually impossible to recognize the presence of inclusions inside (Martínez-Delclòs et al., 2004; Perrichot, 2004). Recently, a new approach for studying amber inclusions within opaque pieces was published, namely X-ray synchrotron radiation using phase propagation contrast (Tafforeau et al., 2006). This technique was later optimized and applied to a large quantity of opaque French Lower Cretaceous amber material from Charentes (Lak et al., 2008a, 2008b), establishing the basis for the study of amber with synchrotron radiation and its later application to different ambers worldwide.

2. Methods

Using third generation synchrotrons, it is possible to obtain a partially coherent X-ray beam due to the small source size and the long distance between the source and the sample (140 meters in the case of the ESRF ID19 beamline). As a result of the coherence, interfaces in the sample create interferential pattern propagation in space. It is then possible to detect enhanced contrast of the sample interfaces just by increasing the distance between the sample and the detector (propagation phase contrast effect). Since the phase contrast effect is far more sensitive than the absorption one, the technique allows for detection of inclusions that would have remained invisible using only absorption contrast (Lak et al., 2008a, 2008b; Tafforeau et al. 2006). This property can be also achieved in some conventional microtomographic devices, but only in small samples at high resolution and low energy (Penney et al., 2007). Nowadays, propagation phase contrast is the most frequently used technique for high-resolution tomographies of inclusions in amber (chiefly performed at the ESRF), with voxel size ranging from 0.35 to 15 μm in the case of larger samples.

The success of the first study (Tafforeau et al., 2006) prompted further development of X-ray synchrotron imaging for other amber inclusions and deposits (e.g., Lak et al., 2008a). Eighty percent of French Cretaceous amber pieces are opaque (Perrichot, 2004), and as such, it is often difficult to know whether there are inclusions within a given piece. To combat this, Lak et al. (2008b) used optimized phase contrast-based microradiographic protocol to survey large quantities of opaque pieces for possible inclusions. Amber pieces were immersed in water to optimize the phase contrast effect by reducing the relative residual absorption contrast. The microradiographs of the opaque blocks were normalized and then surveyed at real resolution size to look for inclusions. Later, select specimens were imaged by propagation phase contrast X-ray synchrotron microtomography (PPC-SRμCT) using local tomography protocol (the amber block being, in most of the cases, far larger than the inclusion itself). Energy was adapted depending upon the size and density pattern of the amber blocks (i.e. presence of pyrite requiring higher energy). Resolution was selected to optimize the level of detail necessary for each inclusion. In some cases, we used a multiscale approach, starting with a complete block tomography (when containing several organisms), followed by detailed scans of selected inclusions, and finishing with higher resolution scans of diagnostic parts of these inclusions.

Using this method of microradiographic survey and later microtomography, more than 350 specimens were recognized inside the blocks of opaque amber from France, thus opening a new window for palaeoentomology.

After acquisition of the scans, the volumes are reconstructed using a filtered back-projection algorithm adapted for local tomography applications (PyHST software, ESRF). The later 3D processing is performed on powerful workstations using the software VGStudioMax (Volume Graphics, Heidelberg, Germany). The segmentation protocol, which virtually extracts the organisms, is based on controlled 3D region growing, fol-

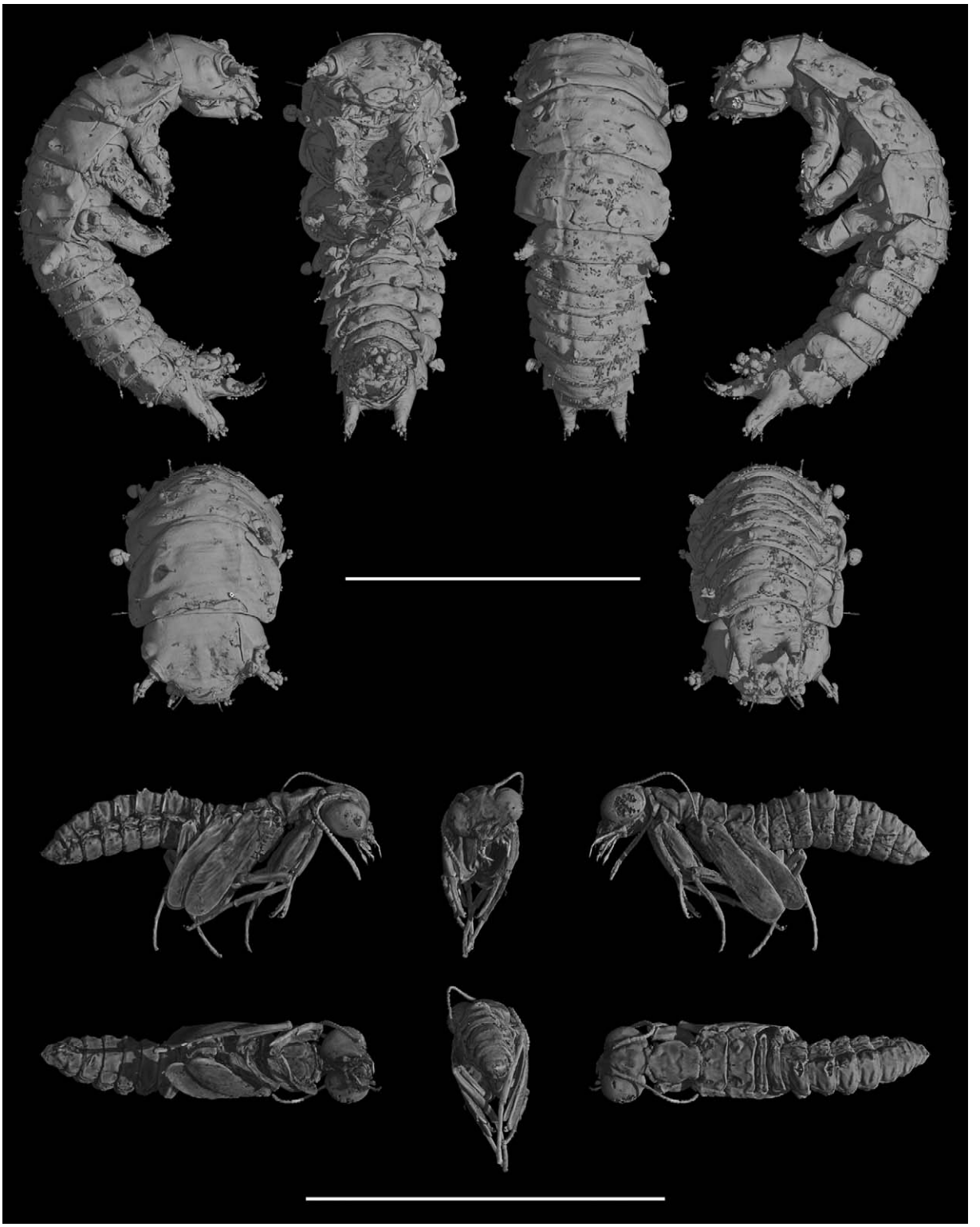

Fig. 1. 3D reconstructions of Lower Cretaceous French amber insects using PPC-SRμCT at ID19 beamline, ESRF, Grenoble. 1: Coleopteran larva, specimen MNHN A33496 (ARC-331.5), voxel size 0.55 μm, propagation distance 70 mm, 35 keV, scale bar 500 μm. 2: Raphidiopteran pupa, specimen MNHN A33497 (ARC-332.1), voxel size 7.46 μm, propagation distance 800 mm, 25 keV, scale bar 5 mm.

Fig. 1. Reconstructions 3D d'insectes dans l'ambre Crétacé inférieur de France, effectuées par PPC-SRμCT sur la ligne de lumière ID19, ESRF, Grenoble. 1 : Larve de Coléoptère, spécimen MNHN A33496 (ARC-331.5), taille de pixel 0,55 μm, distance de propagation 70 mm, 35 keV, barre d'échelle 500 μm. 2 : Pupe de Raphidioptère, spécimen MNHN A33497 (ARC-332.1), taille de pixel 7,46 μm, distance de propagation 800 mm, 25 keV, barre d'échelle 5 mm.

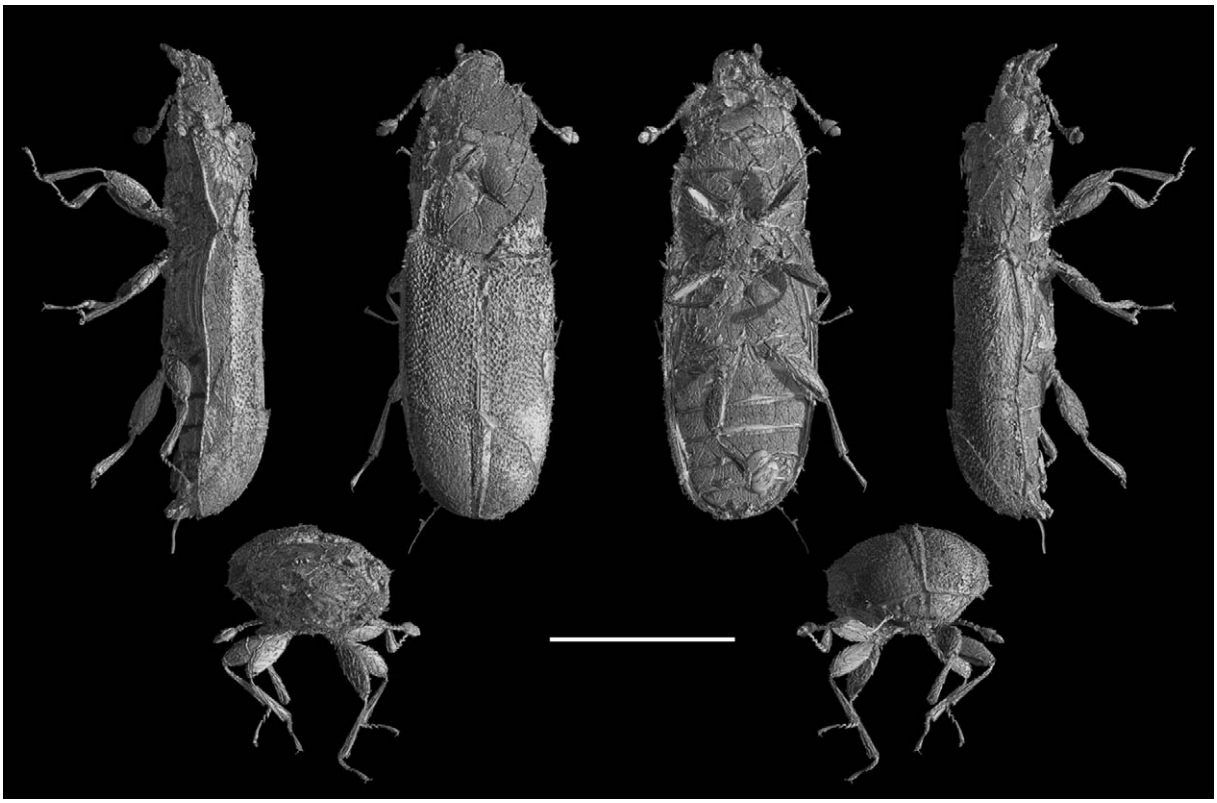

Fig. 2. 3D reconstruction of a monotomid beetle (*Rhizophtoma elateroides* Kirejtshuk et al., 2009), specimen 1512, Coll. D. Azar, from Lower Cretaceous Lebanese amber using PPC-SRμCT at BM05 beamline, ESRF, Grenoble. Voxel size 1.03 μm, propagation distance 50 mm, 20.5 keV. Scale bar 500 μm.
Fig. 2. Reconstruction 3D d'un Coléoptère Monotomidé (*Rhizophtoma elateroides* Kirejtshuk et al., 2009), spécimen 1512, Coll. D. Azar, dans l'ambre Crétacé inférieur du Liban, effectuée par PPC-SRμCT sur la ligne de lumière BM05, ESRF, Grenoble. Taille de pixel 1,03 μm, distance de propagation 50 mm, 20,5 keV. Barre d'échelle 500 μm.

lowed by manual refinement of the rough first result (Fig. 1).

After publication of an exemplar, the microtomographic data is available online in the free access paleontological database at http://paleo.esrf.eu, including original reconstructions of the scan, all the scan parameters, the segmented slices, the VGStudioMax files, .stl surface files for 3D printing, plates and animations with anaglyphic versions. When possible, 3D prints in ABS plus plastic are constructed at the ESRF, which are used as accessible physical representations of the virtual holotypes.

The specimens included in these publications are deposited in the following institutions: French and Lebanese amber at the Division of Palaeontology of the Natural History Museum of Paris (MNHN, France), with French amber being provisionally housed at the Geological Department of the University of Rennes 1 (France); Spanish amber in the Fundación Conjunto Paleontológico Dinopolis (CPT) and in the Museo de Ciencias Nacional de Alava (MCNA), Spain; and Australian amber at the Queensland Museum (Australia).

3. Results

In the last 6 years, amber pieces from virtually the world over have been scanned or surveyed in the ESRF, but long-term projects have been launched only with amber collections from the Cretaceous of France, Spain, and Lebanon, and from the Tertiary of Australia.

The French Cretaceous amber material was the first to be surveyed and microtomographied by synchrotron X-ray imaging (Lak et al., 2008b; Tafforeau et al., 2006), and since the beginning of this work, several hundred plant and animal specimens have been recognized. The French Cretaceous amber outcrops are located mainly in the Southwest of France, and their ages range from Albian to Cenomanian (Néraudeau et al., 2002, 2003, 2005, 2008, 2009; Perrichot and Néraudeau, 2009; Perrichot et al., 2007, 2010).

As noted, the large quantity of opaque amber pieces (approximately 80%) from the Lower Cretaceous French material spurred study using X-ray synchrotron microtomography (Lak et al., 2008a, 2008b). Because synchrotron imaging was first applied to the French deposit, the material has, at this stage, been reconstructed in 3D and published most extensively (Lak et al., 2008b, 2009; Lak

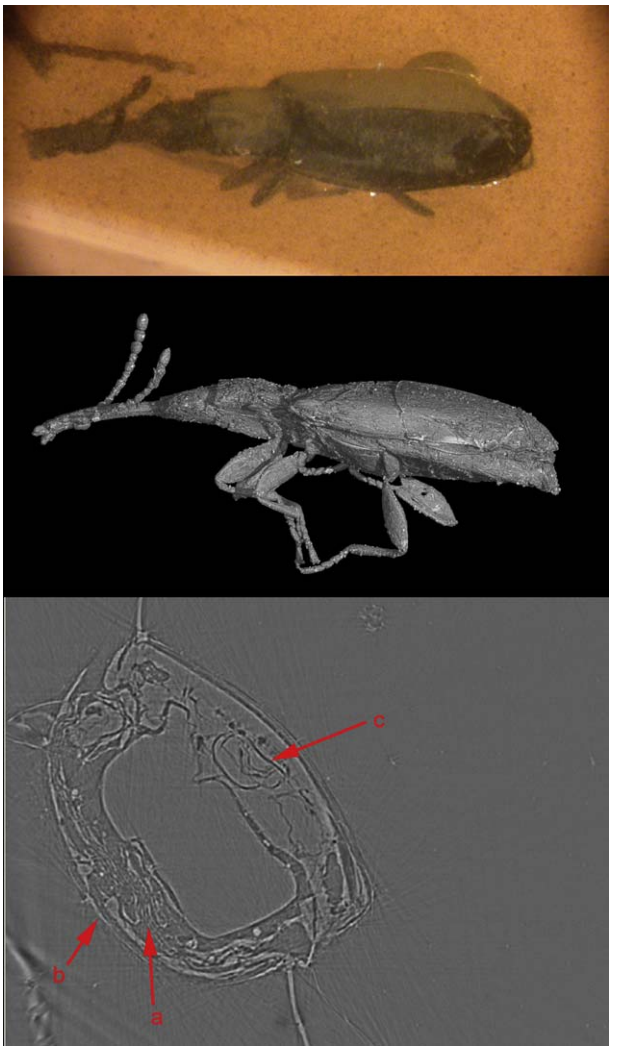

Fig. 3. Coleoptera (Nemonychidae), specimen CPT-4106, from the Lower Cretaceous Spanish amber. 1: Photography of the specimen with binocular. 2: 3D reconstruction of the complete body. 3: Transverse plane projection, showing the hind wings folded (a) and preserved under the elytra (b) and digestive tract (c).
Fig. 3. Coléoptère (Nemonychidae), spécimen CPT-4106, dans l'ambre Crétacé inférieur d'Espagne. 1 : Photo du spécimen à la loupe binoculaire. 2 : Reconstruction 3D du corps complet. 3 : Projection transverse plane montrant les ailes postérieures pliées (a) et préservées sous les élytres (b) et le tube digestif (c).

and Nel, 2009; Perrichot et al., 2008; Tafforeau et al., 2006; Vršanský, 2009).

The latest discoveries from these amber deposits include different larval stages of various groups of insects, including coleopterans and raphidiopterans (Fig. 1). Formal systematic study of these inclusions is complicated because the larval stages of these families do not resemble the adult stages, but they may contribute to the general ecosystem reconstruction. Data from the specimens are available online on the ESRF paleontological database described above. Furthermore, a great number of new larval and adult forms of dipterans, coleopterans, heteropterans, hymenopterans and other groups are currently under study.

Following the success of the French pilot study in late 2008, work began on the Lower Cretaceous amber collection from Lebanon using PPC-SRμCT at the ESRF. Until now, the Lebanese amber deposits, with more than 300 outcrops, are considered to be the oldest with arthropod inclusions (Azar, 2007), and so far numerous representatives of different groups of arthropods, vertebrates and plants have been recognized. Although the amber is fairly transparent, some pieces were surveyed by microtomography to study the internal features of the inclusions and/or to resolve anatomical details invisible with conventional techniques (as was the case, for example, for the oldest representative of the beetle family Monotomidae) (Fig. 2) (Kirejtshuk et al., 2009).

In 2009, a new project studying the fossil content of the Spanish amber outcrops began, and approximately one hundred specimens have already been scanned on the ID19 and BM05 beamlines of the ESRF using PPC-SRμCT. The Spanish amber dates from the Barremian-Cenomanian. The first outcrop with paleobiological content was described in 2000 from Albian deposits (Alonso et al., 2000), and since then several outcrops have been discovered that yield a rich collection of animals and plants (Delclòs et al., 2007; Peñalver et al., 2007; Najarro et al., 2009).

Spanish amber samples are generally translucent, so X-ray synchrotron microradiographic techniques to detect inclusions are not needed. Even so, partial opacity of samples and/or debris within a piece can make the study of morphological details extremely difficult (Fig. 3). In other cases, data on the internal anatomy is required to perform a thorough systematic study. The preservation of internal structures in some Spanish samples has allowed for unprecedented, exhaustive study of the inclusions, for example making it possible to see the hind wings underneath the elytra of beetles (Fig. 3). Other Spanish specimens that have been reconstructed include a female spider of the genus *Orchestina* (family Oonopidae; Fig. 4) and a mymarommatoid wasp of the genus *Gallorommа* (family Gallorommatidae; Fig. 4), both of which are currently under study (e.g., Ortega-Blanco et al., in press).

The Australian Tertiary amber is the newest project currently underway at the ESRF. This material is found on eastern Cape York Peninsula, and although its precise age is the subject of current investigation, its entomological content and geological context suggest a Tertiary age (Bickel, 2009). All the material scanned at the ESRF involved fully opaque pieces; hence the same technique applied to the French Cretaceous opaque amber samples was implemented. From this survey, several arthropod and plant inclusions were recognized, including hymenopterans, hemipterans, dipterans and a diverse group of beetles, some within the family Scolytidae (Fig. 5).

Because of the utility of this method and its relevance for amber research, new projects on other significant amber deposits will begin in the near future at the ESRF.

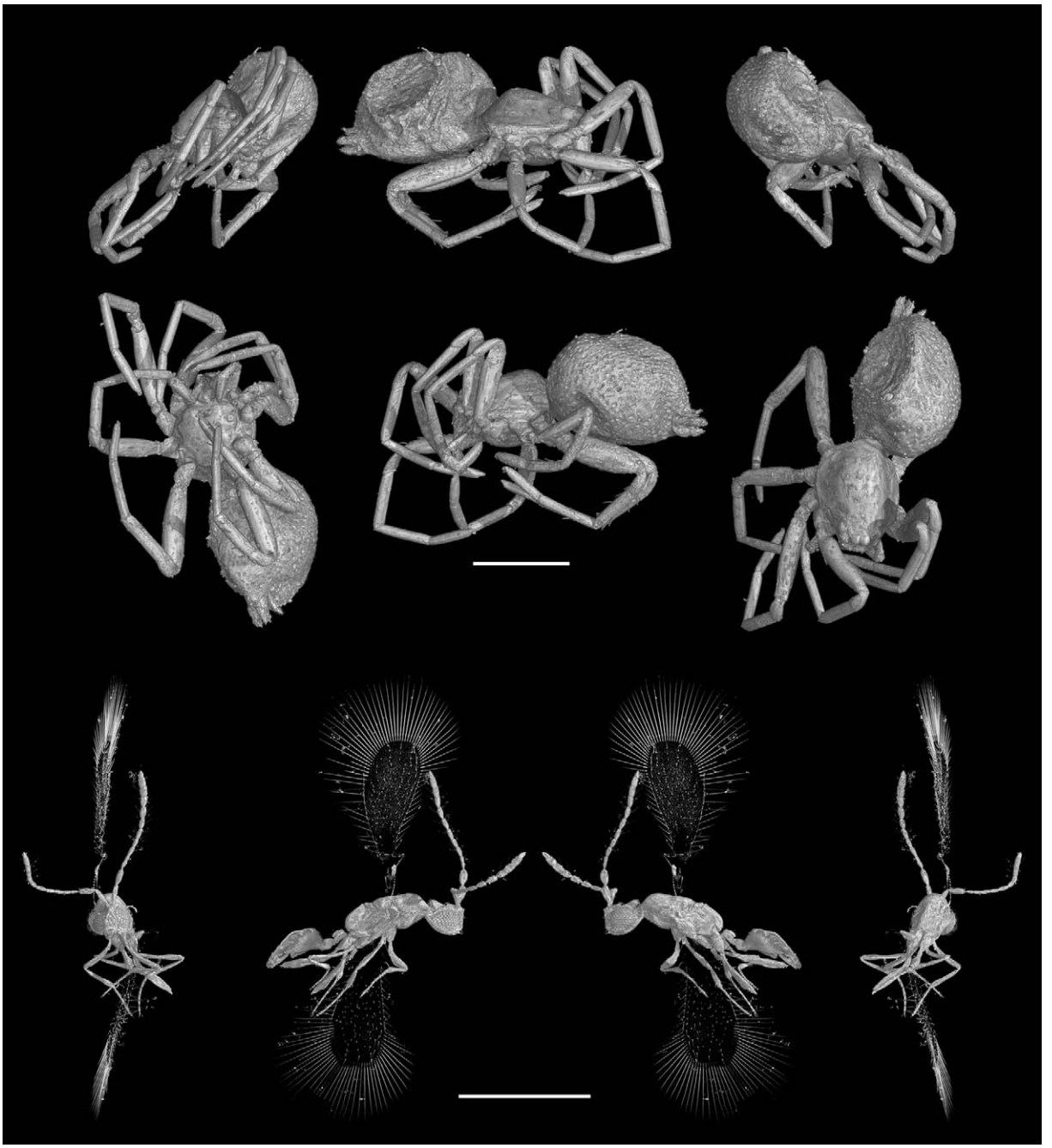

Fig. 4. 3D reconstructions of Lower Cretaceous Spanish amber arthropods using PPC-SRμCT at BM05 beamline, ESRF, Grenoble. 1: Female spider from San Just outcrop (*Orchestina*, Oonopidae), specimen CPT-4100, general habitus, voxel size 0.7 μm, propagation distance 100 mm, 20 keV. Scale bar 500 μm. 2: *Gallorommа* sp., specimen MCNA12630, a wasp of the mymarommatoid family Gallorommatidae from Peñacerrada I outcrop. Voxel size 0.56 μm, propagation distance 25 mm, 25 keV. Scale bar 500 μm.

Fig. 4. Reconstructions 3D d'arthropodes dans l'ambre Crétacé inférieur d'Espagne, effectuées par PPC-SRμCT sur la ligne de lumière BM05, ESRF, Grenoble. 1 : Araignée Oonopidae femelle (*Orchestina* sp.) du gisement de San Just, spécimen CPT-4100, aspect général, taille de pixel 0,7 μm, distance de propagation 100 mm, 20 keV. Barre d'échelle 500 μm. 2 : *Gallorommа* sp., spécimen MCNA12630, guêpe mymarommatoïde de la famille Gallorommatidae du gisement de Peñacerrada I. Taille de pixel 0,56 μm, distance de propagation 25 mm, 25 keV. Barre d'échelle 500 μm.

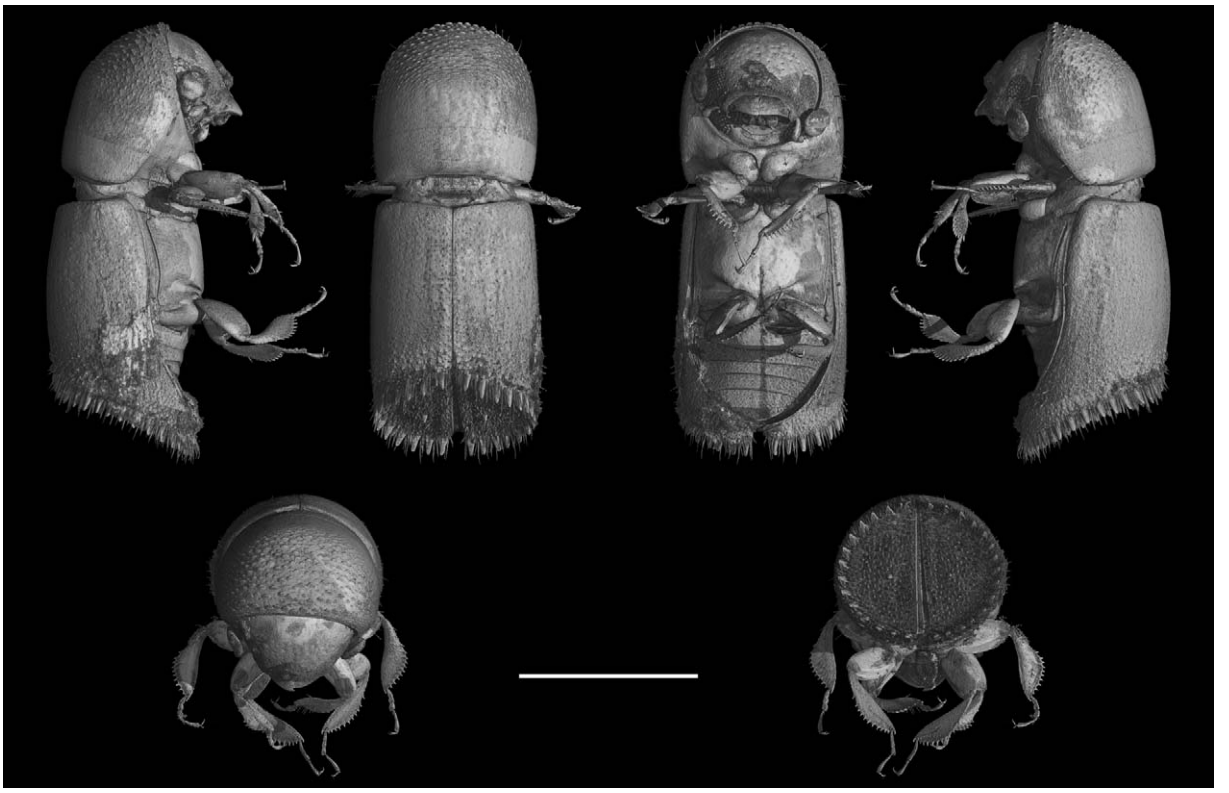

Fig. 5. 3D reconstruction of a scolytid beetle (Scolytidae) from Tertiary Australian amber using PPC-SRμCT at ID19 beamline, ESRF, Grenoble. Voxel size 1.37 μm, propagation distance 150 mm, 30 keV. Scale bar 1 mm.
Fig. 5. Reconstruction 3D d'un Coléoptère Scolytidé dans l'ambre tertiaire d'Australie, effectuée par PPC-SRμCT sur la ligne de lumière ID19, ESRF, Grenoble. Taille de pixel 1,37 μm, distance de propagation 150 mm, 30 keV. Barre d'échelle 1 mm.

All projects are closely related through what is now one of the largest worldwide collaborations on the study of amber.

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Anexo I.5

Biting midges (Diptera: Ceratopogonidae) from the Early Cretaceous El Soplao amber (N Spain)

Ceratopogónidos (Diptera: Ceratopogonidae) del ámbar del Cretácico Inferior de El Soplao (norte de España)

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Resumen:

Se describen tres nuevas especies del yacimiento de ámbar de El Soplao (Rábago, Cantabria, Norte de España), Cretácico Inferior (Albiense Inferior): *Lebanoculicoides excantabris*, *Archiaustroconops borkenti* y *Atriculicoides szadziewskii*. Se identifican en este nuevo yacimiento *Protoculicoides skalskii* Szadziewski & Arillo, hallado en los otros ámbares del Albiense de España de Peñacerrada I (en Burgos) y San Just (en Teruel), y *Austroconops* sp. El hallazgo de una nueva especie del género *Lebanoculicoides* Szadziewski es especialmente relevante en tanto en cuanto este género se considera el más basal conocido de la familia Ceratopogonidae. Hasta la fecha, la nueva especie de *Atriculicoides* Remm representa el registro más antiguo para este género. Se proporciona un resumen general de la taxonomía y la filogenia de la familia Ceratopogonidae, y se muestra la distribución paleogeográfica de sus linajes más basales, subrayando su trascendencia paleoecológica. Los nuevos datos extienden el conocimiento sobre los ceratopogónidos durante el Cretácico Inferior, un periodo clave para comprender las relaciones filogenéticas de los miembros ancestrales de la familia.

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Biting midges (Diptera: Ceratopogonidae) from the Early Cretaceous El Soplao amber (N Spain)

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ABSTRACT

Three new species, *Lebanoculicoides excantabris*, *Archiaustroconops borkenti*, and *Atriculicoides szadziewskii* are described from the Early Cretaceous (early Albian) El Soplao amber deposit (Rábago, Cantabria, northern Spain). *Protoculicoides skalskii* Szadziewski and Arillo, found in the other Albian Spanish ambers from Peñacerrada I (in Burgos) and San Just (in Teruel), and *Austroconops* sp., are identified from this new outcrop. The find of a new species of *Lebanoculicoides* Szadziewski is especially significant since this genus is considered the basalmost known among ceratopogonids. To date, the new species of *Atriculicoides* Remm is the oldest occurrence for this genus. A general review of the taxonomy and phylogeny of the family Ceratopogonidae, and the palaeoecological significance and palaeogeographic distribution of its basalmost lineages are given. The new data extend knowledge about biting midges during the Early Cretaceous, a key period for understanding the phylogenetic relationships of the ancient members of the family.

1. Introduction

Among Diptera, biting midges (Diptera: Ceratopogonidae) are tiny to small nematocerous flies with a wide variety of feeding strategies (haematophagy, predation, nectarivory, pollinivory, and aphagy), and larvae which usually develop in semi-aquatic or moist environments (Borkent, 1995). With nearly 6000 extant species distributed worldwide, biting midges are especially plentiful as amber inclusions, with around 250 extinct species (Borkent, 2011). This abundance is related to the proximity of their habitat to the resin sources, their minute size and their swarming behaviour (Martínez-Delclòs et al., 2004; Grimaldi and Engel, 2005). The abundant fossil diversity in widespread amber deposits, which range from the Cretaceous to the Miocene, renders ceratopogonid flies highly suitable organisms on which to carry out phylogenetic studies and thus to extract evolutionary patterns (Borkent, 2000a, Fig. 23).

A new Spanish amber deposit was recently discovered in El Soplao, near the municipality of Rábago (Cantabria, northern Spain) (Najarro et al., 2009). Notable features of this outcrop include the plentiful presence of amber pieces with a blue-violet glow, a fluorescence conferred by certain organic compounds (Menor-Salván et al., 2009a, b, 2010), and its special richness in amber formed by resin exuded under aerial conditions (stalactite-shaped flows and other flows, like crusts). Amber pieces with stalactitic or flow morphology and an inner banding pattern as a result of succesive resin flows probably originated from aerial polymerised resin. This kind of amber contains a large quantity of bioinclusions, especially small flying insects, due to its high degree of exposure (Martínez-Delclòs et al., 2004). Geological and palaeobiological data indicate that the amber deposit had a para-autochthonous origin in which wildfires promoted both resin production and erosion (Najarro et al., 2010). Moreover, biochemical data suggest that El Soplao amber was generated by resin exuded by two different coniferous sources (Menor-Salván et al., 2009a, 2010). Initial studies of El Soplao amber have provided bioinclusions related to spiders and insects from 11 orders: Blattaria, Isoptera, Psocoptera, Thysanoptera, Hemiptera, Raphidioptera, Neuroptera, Coleoptera, Hymenoptera, Diptera, and Trichoptera. To date, the insects described include one new species of the thysanopteran family Thripidae (Nel et al., 2010), one new genus and species of the Jurassic-Cretaceous raphidiopteran family Mesoraphidiidae (Pérez-de la Fuente et al., 2010), and one new

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species of the hymenopteran family Serphitidae (Ortega-Blanco et al., 2011).

Here, we describe three new ceratopogonid species from El Soplao amber and report one genus and one species previously known from other Cretaceous Spanish ambers. This paper also discusses their likely habitats and feeding habits, giving an overview of the taxonomy and phylogeny of the Ceratopogonidae, as well as the palaeogeographic distribution of its ancient lineages.

2. Geological setting

El Soplao is located on the north-west margin of the Basque-Cantabrian Basin. The development of the basin during the Early Cretaceous is related to the kinematics between the European and Iberian plates (Malod and Mauffret, 1990; Olivet, 1996). The El Soplao amber-bearing deposit, early Albian in age, is included within the Las Peñosas Formation, in a unit of heterolithic sandstones-siltstones and carbonaceous mudstones related to broadly coastal delta-estuarine environments (Najarro et al., 2009). In fact, the El Soplao deposit comprises part of the strip curve formed from most of the previously known Spanish amber outcrops, corresponding to the coastline during the Early Cretaceous (Delclòs et al., 2007). A 0.7–2.5 m thick level of organic-rich clays contains the amber pieces, together with plant cuticle remains mainly belonging to the conifer genera *Frenelopsis* (Schenk, 1869) emend. Watson, 1977 and *Arctopitys* Bose and Manum, 1990. Gingkoalean leaves of *Eretmophyllum* Thomas, 1913 (formerly cited for this outcrop as *Nehvizdya*) and *Pseudotorellia* Florin, 1936 are found as well. Palinological information that completes the overview of the palaeoforest is given in Najarro et al. (2010), and extensive stratigraphical and sedimentological information of the El Soplao amber-bearing outcrop is provided by Najarro et al. (2009).

3. Material and methods

The ceratopogonid inclusions were found in amber collected when the outcrop was discovered in 2007, and in three consecutive excavations. Amber pieces containing the samples were included in synthetic Epoxy resin (EPO-TEK 301) and then polished (extensive protocol is given in Corral et al., 1999).

The number ES-07-xx was assigned to those ceratopogonid specimens provisionally housed at the "Museo Geominero" (IGME) in Madrid (Spain), whilst those that will be housed at the future El Soplao museum in Cantabria (Spain) were given the number CES-xxx.

Fossils were examined with a Leica MS5 binocular microscope and a Zeiss Axiophot optical microscope. General photographs were taken using a Leica DFC420 camera. Microphotographs were obtained with the aid of a Sony DXC-S500 digital camera attached to the microscope. Drawings were made using a camera lucida. Measurements were obtained using the Leica IM1000 programme. Some images were reconstructed using Combine Z5 computer software.

Terminology and criteria for measuring follow those of Borkent (1995, 2000a).

4. Taxonomy and phylogeny of the Ceratopogonidae

The major lineages conforming the order Diptera, although still controversial in some phylogenetic aspects, are nowadays consistently defined (the most recent review of the high-level phylogeny of Diptera is given in Yeates et al., 2007). The Ceratopogonidae form part of the lower Diptera, formerly known as the suborder "Nematocera", now that its paraphyletism has been accepted (state of the art phylogenetic interpretations of lower Diptera are given in Bertone et al., 2008). The nematocerous flies, and thus the whole Diptera order, would have separated from their mecopteroid ancestor around the Permo-Triassic boundary, although the first true dipteran record is not reported until the Lower/Middle Triassic of France (Krzemiński and Krzemińska, 2003). Moreover, biting midges are classified within the infra-order (or suborder *sensu* Amorin and Yeates, 2006) Culicomorpha Hennig, 1973, monophyletically grouping most of the blood-feeding nematocerous dipterans (Grimaldi and Engel, 2005). The oldest known culicomorphan, *Aenne triassica* Krzemiński and Jarzembowski, 1999 comes from the Late Triassic of England (Krzemiński and Jarzembowski, 1999). This Triassic genus belongs to the Chironomidae (non-biting midges), which could be considered the sister group of Ceratopogonidae (Beckenbach and Borkent, 2003).

The patterns of diversification obtained with morphological and molecular analyses of extant taxa have revealed a strong correlation with the fossil record of Ceratopogonidae, the monophyly of which is widely accepted (Borkent, 2000a; Beckenbach and Borkent, 2003; Borkent and Craig, 2004). The family is today divided into five subfamilies: Ceratopogoninae Newman, 1834; Leptoconopinae Noé, 1907; Dasyheleinae Lenz, 1934; Forcipomyiinae Lenz, 1934, and Lebanoculicoidinae Borkent, 2000 (Borkent, 2011). A first, basal group of lineages was already established in the Old World during the Early Cretaceous, but may possibly have started in the Late Jurassic (Fig. 1). It is composed of genera mainly classified in the subfamily Leptoconopinae and the monogeneric subfamily Lebanoculicoidinae, which is the only subfamily without extant representatives. The genus *Lebanoculicoides* Szadziewski, 1996, hitherto exclusively reported from the late Barremian–Aptian Lebanese amber (Szadziewski, 1996), is considered the sister group of all the remaining Ceratopogonidae in that it is the only biting midge to retain fully developed R_1, R_3 and R_{4+5} wing veins. This important feature justified the creation of its own subfamily (Borkent, 2000a). In turn, the subfamily Leptoconopinae includes six genera that would have shared a common ancestor (Borkent and Craig, 2004). Four of these are extinct, *Minyohelea* Borkent, 1995, *Archiaustroconops* Szadziewski, 1996, *Fossileptoconops* Szadziewski, 1996, and *Jordanoconops* Szadziewski, 2000; the two remaining genera, *Leptoconops* Skuse, 1889, and *Austroconops* Wirth and Lee, 1958, currently surviving as relicts (Szadziewski, 2008; more information in section 6), are today the only extant representatives of the initial ancient diversity of the family. However, there are some basal, Early Cretaceous genera with uncertain phylogenetic position, e.g. *Protoculicoides* Boesel, 1937 and *Atriculicoides* Remm, 1976. Neither genus shows autapomorphies, and their diagnosis is mainly based on characters that are highly subject to homoplasy (e.g. mid-dorsal separation/union between the eyes and presence/absence of macrotrichia on the wing membrane), which have therefore been discarded for phylogenetic tests (Borkent, 1995, 2000a; Szadziewski, 1996; Borkent and Craig, 2004). Thus, these cladistic inferences, although consistent as a whole, have necessarily been based on the use of symplesiomorphies to locate *Protoculicoides*, and primarily on poorly conspicuous characters such as synapomorphies for placing *Atriculicoides*, having been reported from a scarce fossil diversity of the genus. However, *Protoculicoides* remains unclassified at subfamily level, and uncertainty exists as to whether it belongs to the monophyletic Leptoconopinae or the

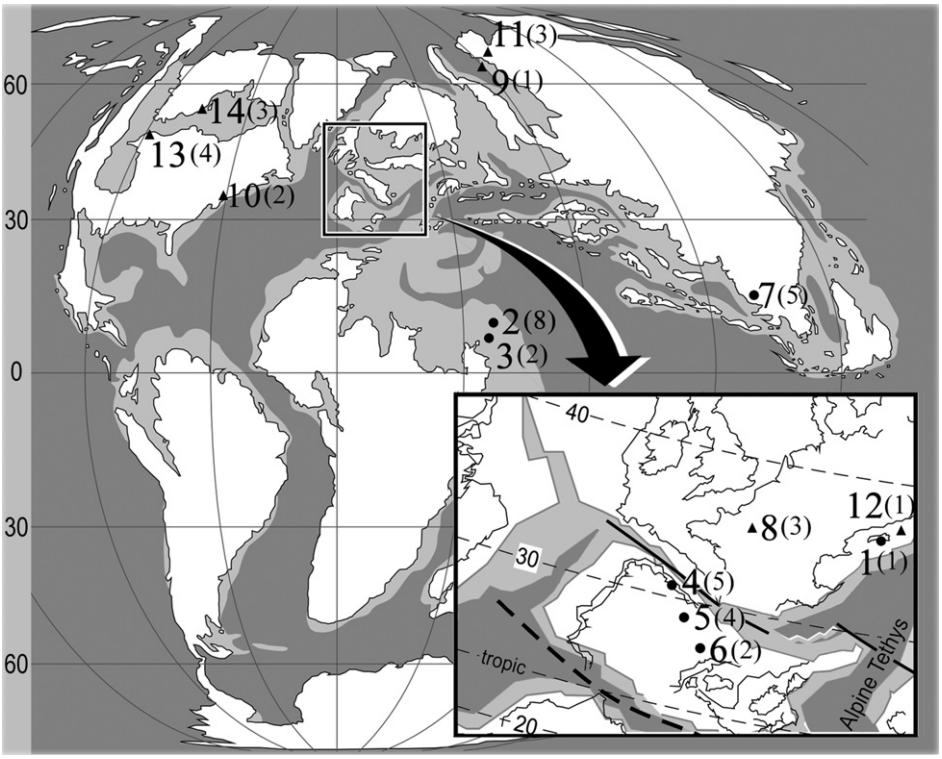

Fig. 1. Distribution among Early to Late Cretaceous ambers of the described Ceratopogonidae belonging to the most ancient lineages of the family, already present during the Early Cretaceous. The palaeogeographic map (redrawn from Blakey, 2008), corresponds to middle Albian (~105 Ma). The framed area (Southwestern Europe) is amplified at the bottom right of the figure. Early and Late Cretaceous ambers are indicated by dots and triangles respectively. The number of genera found for each amber deposit is indicated in brackets. Data extracted essentially from Borkent (2011) and complemented by information in Borkent (1995), Szadziewski (1996, 2000, 2004), Borkent (2000a, b), Szadziewski and Arillo (2003), Arillo et al. (2008), Poinar (2008) and this paper. Although ceratopogonids have been well reported from French amber (Szadziewski and Schlüter, 1992; Perrichot, 2004; Perrichot et al., 2007), their detailed study has not yet begun, and thus they are under-represented in the figure. Note also how the coincidence of biting midges has contributed to the correlation of Campanian Canadian ambers (McKellar et al., 2008). **Early Cretaceous ambers**. (1) Austria (Hauterivian): *Minyohelea casca*. (2) Lebanon (late Barremian–Aptian): *Archiaustroconops ceratoformis*, *A. cretaceous*, *A. bocaparvus*, *A. hamus*, and *A. szadziewskii*. *Archiculicoides acraorum*, *A. schleei*, and *A. unus*. *Austroconops fossilis*, *A. gladius*, *A. gondwanicus*, and *A. megaspinus*. *Fossileptoconops lebanicus*. *Lebanoculicoides mesozoicus*. *Leptoconops* (*Palaeoconops*) *amplificatus* and *L.* (*P.*) *antiquus*. *Minyohelea bacula*, *M. falcata*, *M. lebanica*, *M. minuta*, *M. schleei*, and *M. wirthi*. *Protoculicoides succineus* and *P. punctus*. (3) Jordan (Albian): *Archiaustroconops* sp. *Jordanoconops weitschati*. Spanish ambers. (4) El Soplao, Cantabria (early Albian): *Archiaustroconops borkenti* sp. nov. *Atriculicoides szadziewskii* sp. nov. *Austroconops* sp. *Lebanoculicoides excantabris* sp. nov. *Protoculicoides skalskii*. (5) Peñacerrada I, Burgos (early Albian): *Archiaustroconops alavensis*. *Austroconops* sp. *Leptoconops zherikhini*. *Protoculicoides skalskii*. (6) San Just, Teruel (middle Albian): *Leptoconops zherikhini*. *Protoculicoides skalskii*. (7) Myanmar (late Albian–Cenomanian): *Archiaustroconops gracilis* and *A. kotejai*. *Atriculicoides swinhoei*. *Austroconops asiaticus*. *Leptoconops burmiticus*, *L. myanmaricus*, *L. nosopheris*, *L. rossi*, and *L. subrossicus*. *Protoculicoides burmiticus*. **Late Cretaceous ambers**. (8) Northwestern France (Cenomanian): *Atriculicoides cenomanensis* and *A. incompletus*. *Austroconops borkenti*. *Leptoconops* sp. (9) Nizhnyaya Agapa, Taimyr (Cenomanian): *Leptoconops boreus*. (10) New Jersey (Turonian): *Atriculicoides globosus* and *A. incompletus*. *Leptoconops copiosus* and *L. curvachelus*. (11) Yantardakh, Taimyr (Coniacian–Santonian): *Atriculicoides macrophthalmus*, *A. dasyheleis*, *A. sibiricus*, and *A. taimyricus*. *Austroconops sibiricus*. *Leptoconops sibiricus* and *L. boreus*. (12) Hungary (Coniacian–Santonian): *Leptoconops clava*. Canadian amber (Campanian). (13) Grassy Lake, Alberta: *Atriculicoides globosus*. *Minyohelea pumilis*. *Leptoconops primaevus*. *Protoculicoides depressus*. (14) Cedar Lake, Manitoba: *Atriculicoides globosus*. *Leptoconops primaevus*. *Protoculicoides depressus*.

[Forcipomyiinae + Dasyheleinae + Ceratopogoninae] clade (Borkent and Craig, 2004). *Atriculicoides* has provisionally been classified within the subfamily Forcipomyiinae since Borkent (1995), and is the sister group to a clade grouping Forcipomyiinae and Dasyheleinae (which would be tribes according to Szadziewski, 1996). On the other hand, more derived lineages of Ceratopogonidae have successfully diversified worldwide since the Late Cretaceous. They mostly correspond to taxa classified within the subfamily Ceratopogoninae, but also within the subfamilies Dasyheleinae and Forcipomyiinae. An updated Ceratopogonidae species catalogue is given in Borkent (2011).

5. Systematic palaeontology

Order: Diptera Linnaeus, 1758
Infraorder: Culicomorpha Hennig, 1973 (see also Amorin and Yeates, 2006)
Family: Ceratopogonidae Newman, 1834
Subfamily: Lebanoculicoidinae Borkent, 2000
Genus *Lebanoculicoides* Szadziewski, 1996

Type species. *Lebanoculicoides mesozoicus* Szadziewski, 1996.

Range and locality. Early Cretaceous (late Barremian–Aptian) Lebanese amber (Jezzine).

Lebanoculicoides excantabris sp. nov.
2009 *Lebanoculicoides* sp. Najarro et al., p. 382, Fig. 13.

Material. Single female (holotype), ES-07-9. The specimen was found together with two wasps (Hymenoptera), a mymarommatid (ES-07-8) and a platygastrid (ES-07-10), as syninclusions. Head and scutum are depressed and the thorax is compressed. Unfortunate position of the legs prevents accurate observation of the genitalia.

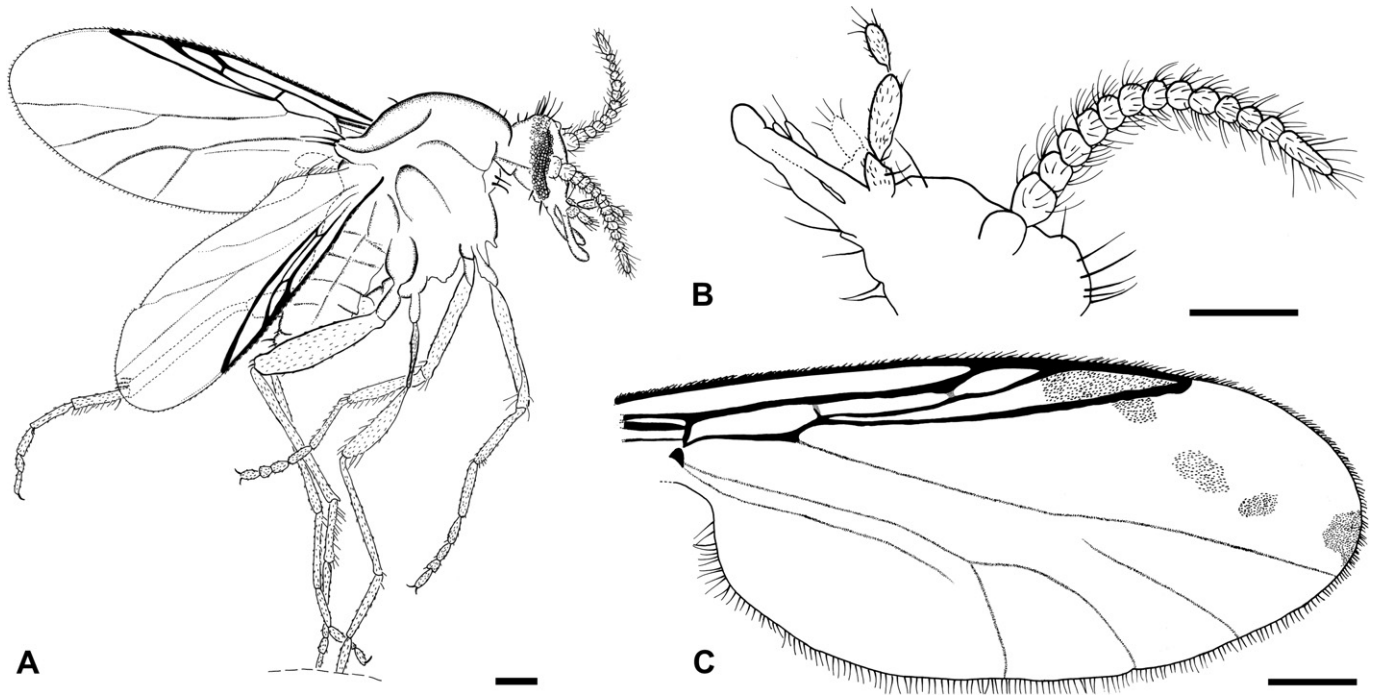

Fig. 2. Camera lucida drawings of *Lebanoculicoides excantabris* sp. nov., holotype ES-07-9. A, lateral habitus. B, head in lateral view. C, left wing. Scale bars = 0.1 mm.

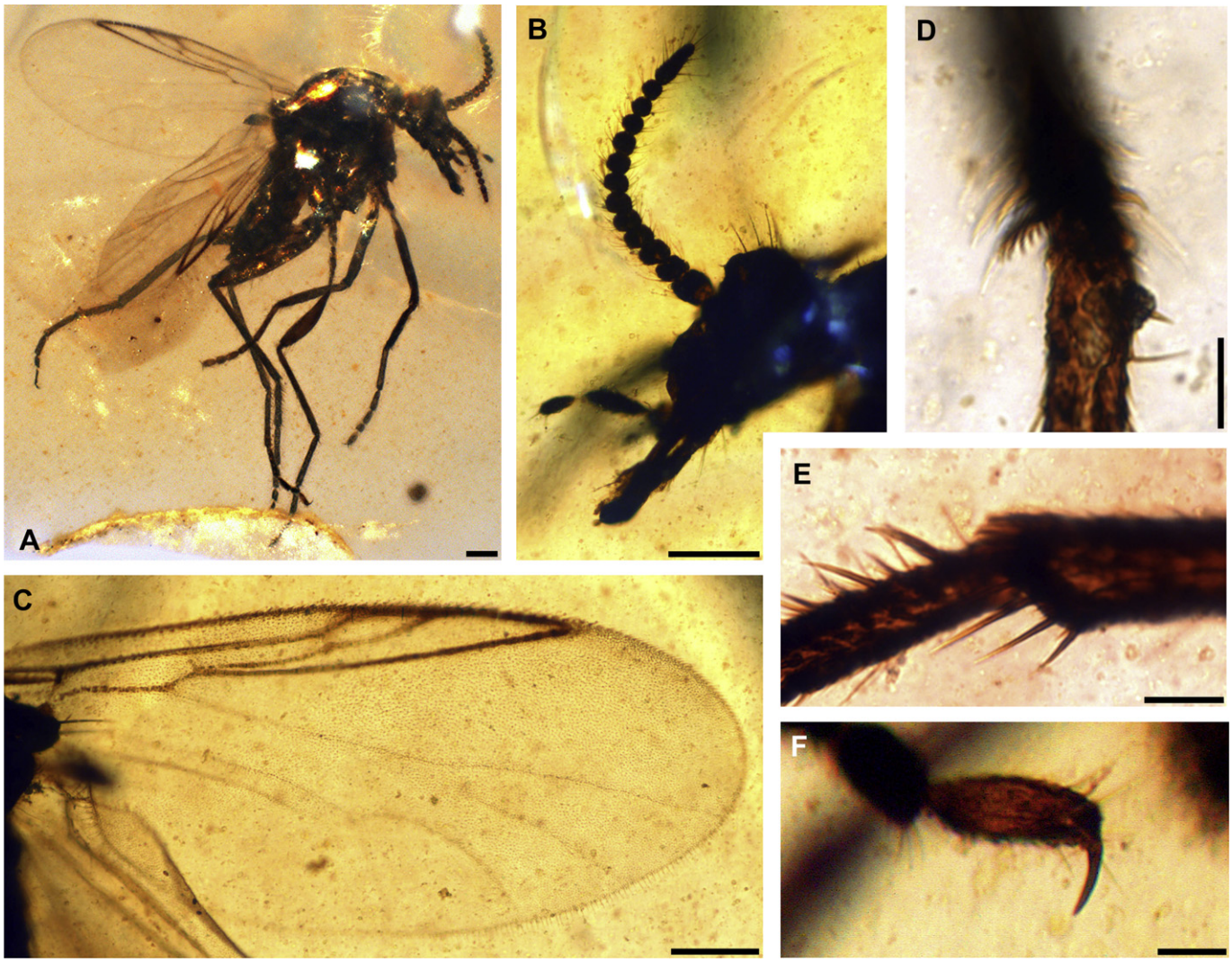

Fig. 3. *Lebanoculicoides excantabris* sp. nov., holotype ES-07-9. A, lateral habitus. B, lateral view of head. C, left wing. D, right foreleg tibio-tarsal articulation. E, left hindleg tibio-tarsal articulation. F, left hindleg tarsal claws. Scale bars. A–C = 0.1 mm; D–F = 0.025 mm.

Derivation of name. Latin *ex Cantabris*, meaning "from the land of Cantabria".

Diagnosis. *Male*. Unknown. *Female*. Short flagellomeres (not elongated); palpus 4-segmented; R_{4+5} terminating in a basal position before reaching the wing apex.

Description. Female (Figs. 2A and 3A). Total length = 0.98 mm. *Head*. Eye separation poorly visible. Antenna with 13 separate flagellomeres ovoidal to subspherical towards the apex, terminal flagellomere elongated (Figs. 2B and 3B). Mouthparts elongated; mouthpart length/length of fifth tarsomere of foreleg = 3.6. Palpus 4-segmented; segment 3 slightly swollen; segments 3/4 + 5 = 1.6 (Figs. 2B and 3B). *Thorax*. Scutum setose. Scutellum rounded, with a few long thick setae along its margin. *Wing*. Length = 0.92 mm, costal ratio = 0.76. Without macrotrichia; microtrichia present in the entire wing membrane. Costa (C) not extending beyond apex of radial veins 4 + 5 (R_{4+5}). Two radial cells well-developed; first radial cell 1.5 times longer than the second. R_{4+5} well-developed, reaching wing margin well before the wing apex (Figs. 2C and 3C). Transverse vein r-m oblique, not subperpendicular to C. Media (M) petiolate. Vein M_2 basally absent. *Legs*. Slender. Foreleg tibiae with a pectinated tibial spur (Fig. 3D); midleg tibiae with apical spur; hindleg tibiae with single transverse row of apical spines (= tibial comb, Fig. 3E). Hindleg 1st tarsomere with scattered spines (Fig. 3E). Thick, paired spines in apex of tarsomeres 1–4. Tarsal ratio of foreleg = 1.9, hindleg = 1.2, foreleg/hindleg = 1.6. Claws short, simple, similar in all legs (Fig. 3F). *Genitalia*. Cerci elongated, about twice as long as wide.

Remarks. After Szadziewski (1996) described the genus based on one female, Borkent (2000a) reported the male and simplified the diagnosis to one unique character: the presence of a fully developed R_1, R_3, and R_{4+5}. Whereas in *Lebanoculicoides mesozoicus* R_{4+5} is concave and almost reaches the wing tip, in *Lebanoculicoides excantabris* sp. nov. it is convex and clearly ends some distance from the wing tip. In addition to the diagnostic characters, a quite low hindleg tarsal ratio and the cerci length also differentiate these two species. It is noteworthy that the elongated cerci of *L. excantabris* should recall those of *Leptoconops* Skuse, 1889.

Subfamily indet.
Genus *Protoculicoides* Boesel, 1937

Type species. *Protoculicoides depressus* Boesel, 1937.

Range and locality. Early to Late Cretaceous (late Barremian–Campanian). *Protoculicoides succineus* Szadziewski, 1996, and *Protoculicoides punctus* Borkent, 2000 from late Barremian–Aptian Lebanese amber; *Protoculicoides skalskii* Szadziewski and Arillo, 1998 from early Albian Peñacerrada I amber (Spain); *Protoculicoides burmiticus* Szadziewski and Poinar, 2005 from late Albian–Cenomanian Burmese (Myanmar) amber; *Protoculicoides depressus* Boesel, 1937 from Campanian Canadian amber.

Protoculicoides skalskii Szadziewski and Arillo, 1998.

Material. Single female, ES-07-18.

Description. Female (Fig. 4). Total length = 1.35 mm. *Head*. Compound eyes separated mid-dorsally. Single vertex seta not visible. Antenna with 13 separate flagellomeres; flagellomeres 9–13 more elongated than those preceding them, gradually increasing in length towards the apex. Mouthparts very elongated, about twice as long as the eye height; mouthpart length/length of fifth tarsomere of foreleg = 6.4. Palpus 5-segmented; segment 3 very elongated, cylindrical; segments 4 and 5 subequal in length. *Thorax*. Scutum and scutellum with elongated setae. Scutellum with rounded apex. *Wing*. Length = 1.15 mm, costal ratio = 0.84. Single row of macrotrichia at dorsal margins of C and radius (R). Wing

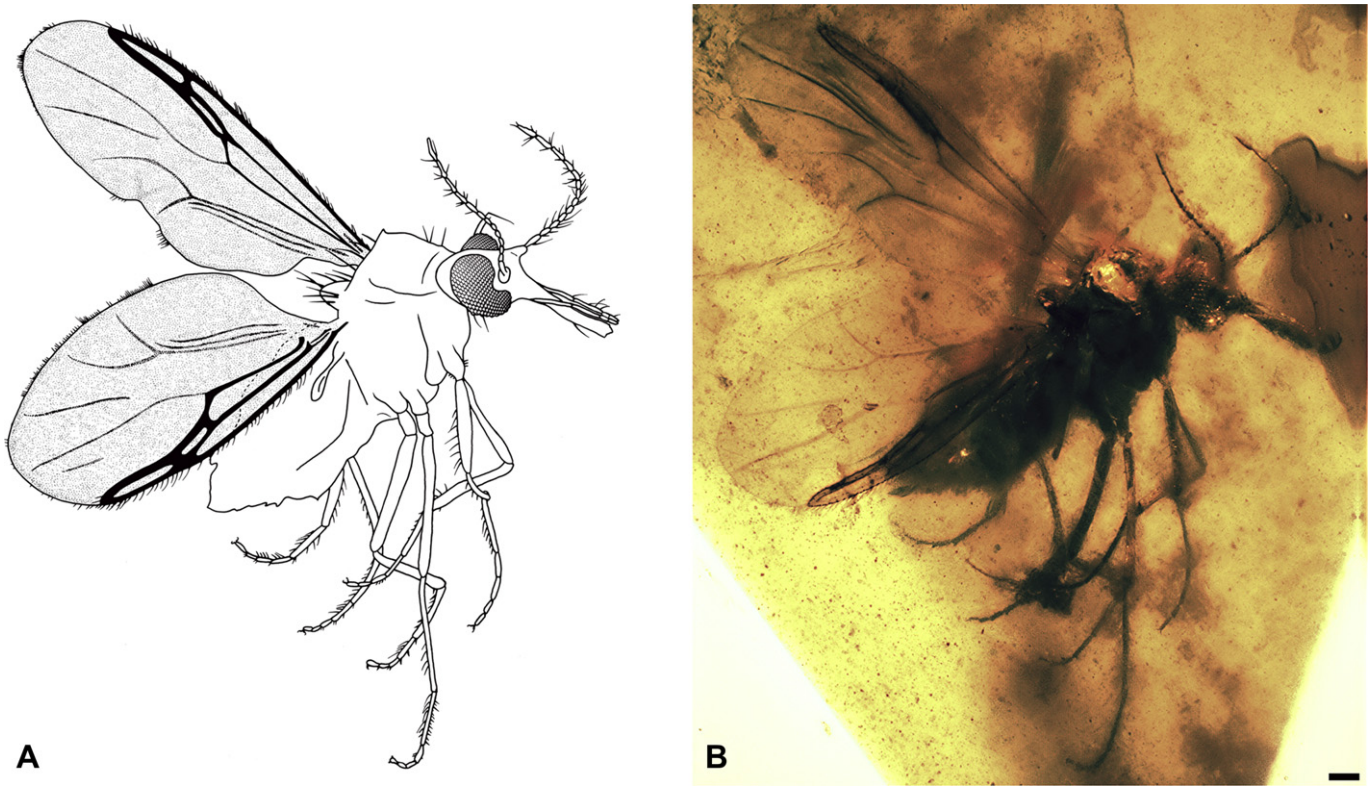

Fig. 4. *Protoculicoides skalskii* Szadziewski and Arillo, 1998, ES-07-18. A, camera lucida drawing. B, photograph. Scale bar = 0.1 mm.

membrane without macrotrichia, microtrichia distinct. C ending at tip of vein R_3. Two well-developed radial cells present, rounded; second radial cell longer than the first. Transverse vein r-m oblique. M petiolate. Vein M_2 basally absent. *Legs.* Slender. Pair of thick setae not visible on fore- and midleg trochanter. Foreleg tibiae with two slender tibial spurs; midleg tibial spur not present; hindleg tibiae with single transverse row of apical spines (= tibial comb). Mid- and hindleg first and second tarsomeres with scattered, stout spines (better defined in first tarsomere). Thick, paired spines at apex of tarsomeres 1–4 conspicuous only in mid- and hindlegs. Tarsal ratio of foreleg = 1.9, hindleg = 2.1, foreleg/hindleg = 0.9. Claws short, simple, similar in all legs, somewhat basally widened. *Genitalia.* Barely visible.

Remarks. The specimen ES-07-18 is a member of the genus *Protoculicoides* on the basis of the presence of two well-developed radial cells, the absence of a well-defined R_{4+5}, a wing membrane devoid of macrotrichia, a costal ratio > 0.7, and a foreleg/hindleg tarsal ratio < 1.3 (Borkent, 2000a).

It is assigned to *P. skalskii* by the following characters: (a) the very elongated mouthparts, (b) the cylindrical morphology of the palpal segment 3, and (c) a C not extending beyond apex of R_3. This species was described from Peñacerrada I but was also reported from San Just (Arillo et al., 2008), both localities in Spain (Alonso et al., 2000; Peñalver et al., 2007). Although genitalia are not clearly visible in this specimen owing to amber fractures, it is interpreted as a female because of antennal features that have been observed repeatedly within the fossil diversity of the genus (and also other ancient Cretaceous genera such as *Atriculicoides*): the last five flagellomeres are elongated (instead of the last three or four in males) and the well-developed plume of setae typical of males is not present. The ES-07-18 specimen has a relatively higher costal ratio than the holotype, which could be interpreted as intraspecific variability (0.84 vs. 0.73).

Subfamily: Leptoconopinae Noé, 1907 (=Austroconopinae Borkent and Craig, 2004)
Genus *Archiaustroconops* Szadziewski, 1996

Type species. *Archiaustroconops ceratoformis* Szadziewski, 1996.

Range and locality. Early Cretaceous (late Barremian–Cenomanian). *Archiaustroconops ceratoformis* Szadziewski, 1996, *A. cretaceous* (Szadziewski, 1996), *A. bocaparvus* Borkent, 2000, *A. hamus* Borkent, 2000 and *Atriculicoides szadziewskii* Borkent, 2000 from late Barremian–Aptian Lebanese amber; *Archiaustroconops alavensis* Szadziewski and Arillo, 1998 from early Albian Peñacerrada I amber (Spain); *Archiaustroconops gracilis* Szadziewski and Poinar, 2005 and *A. kotejai* Szadziewski and Poinar, 2005 from late Albian–Cenomanian Burmese (Myanmar) amber.

Archiaustroconops borkenti sp. nov.
2009 *Archiaustroconops* sp. Najarro et al., p. 381, Fig. 12E.

Material. Single female (holotype), ES-07-17. The specimen is well-preserved, but the thorax is ventrally compressed and the abdomen is strongly deformed and partially burst on the left side. A globular artefact (probably a gas bubble) connects with the abdomen.

Derivation of name. The species name is dedicated to Dr Art Borkent, in recognition of his prominent contribution to the knowledge of biting midges.

Diagnosis. Male. Unknown. *Female*. Eyes separated mid-dorsally; elongated flagellomeres; palpus 5-segmented with segment 3 greatly swollen and laterally flattened; C extending beyond apex of R_3 along almost the total wing length, elongated first radial cell.

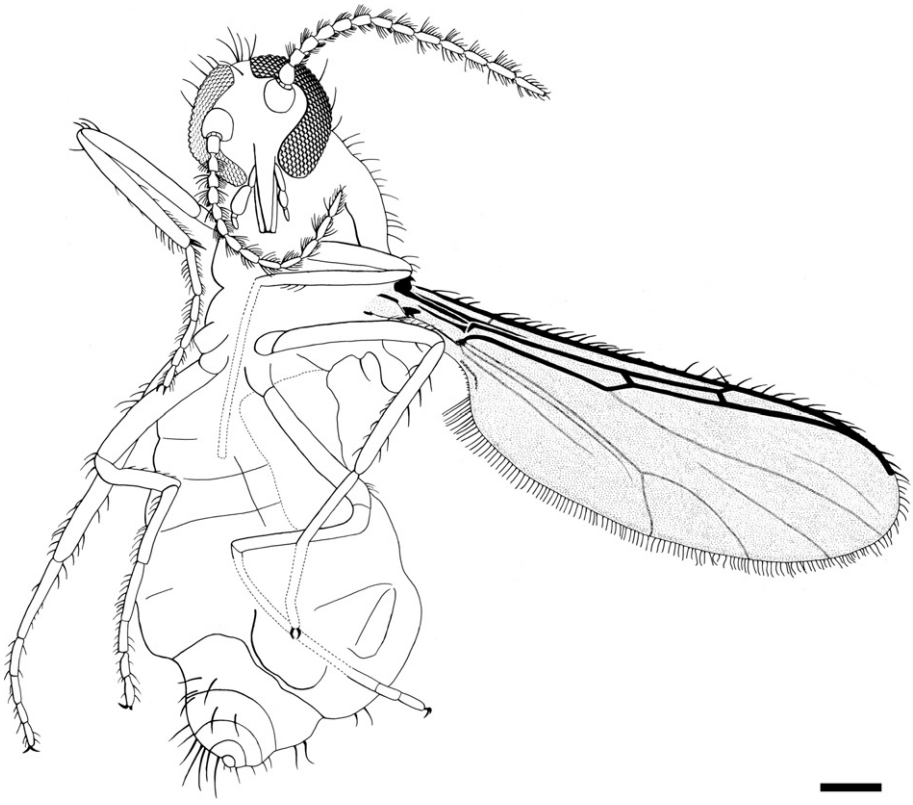

Fig. 5. Camera lucida drawing of the ventral habitus of *Archiaustroconops borkenti* sp. nov., holotype ES-07-17. Scale bar = 0.1 mm.

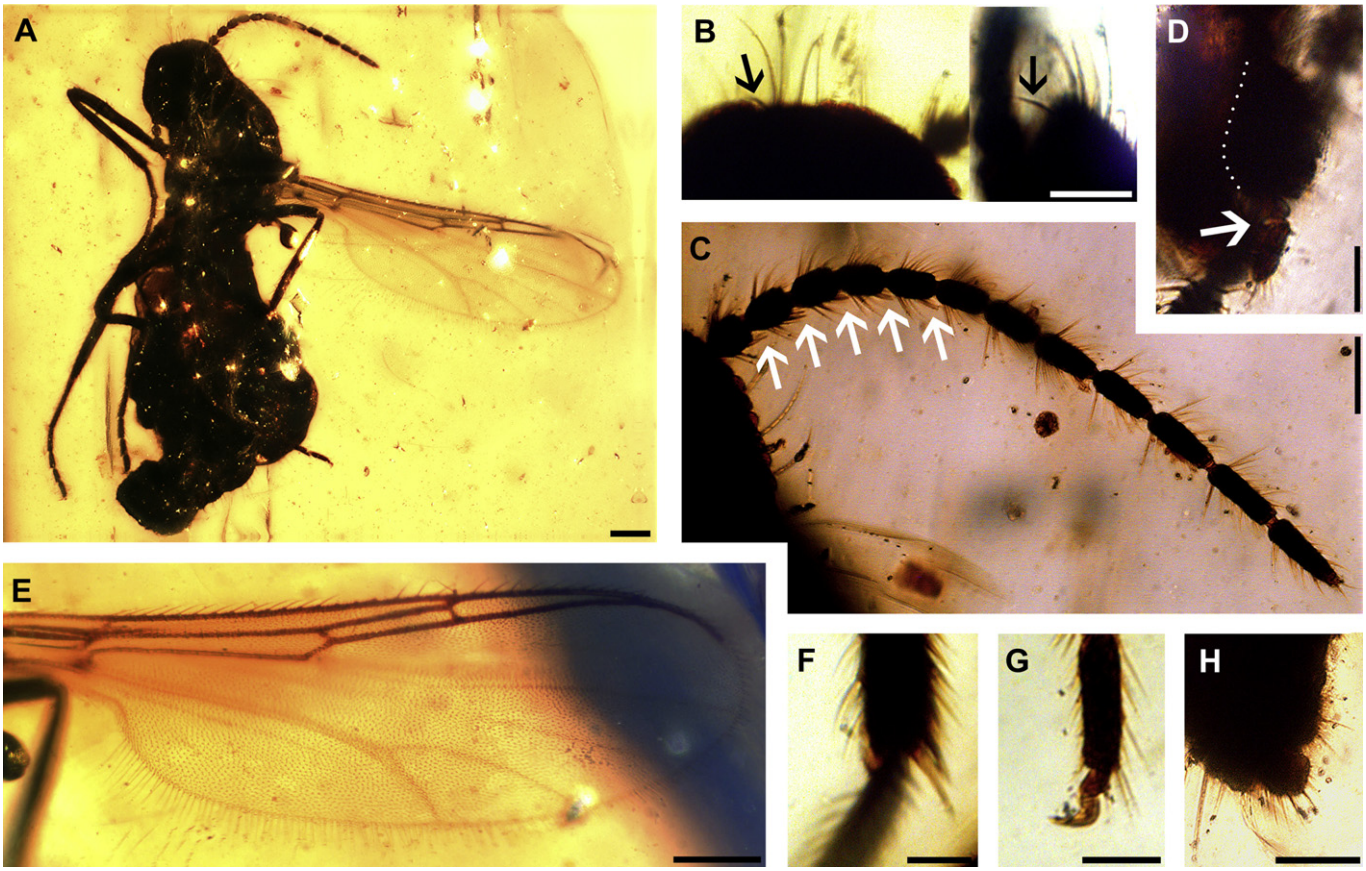

Fig. 6. *Archiaustroconops borkenti* sp. nov., holotype ES-07-17. A, ventral habitus. B, frontal (left) and lateral (right) views of dorsal part of head. Arrow points to the separation between composite eyes which bears the single vertex seta. C, flagellomeres 2–13 of the left antenna. Arrows show sensilla trichoidea in the basad flagellomeres. D, right palpus in lateral view. Silhouette of the palpal segment 3 has been partially highlighted. Arrow shows the separation between palpal segments 4 and 5. E, left wing. F, right foreleg tibio-tarsal articulation. G, tarsal claws of left hindleg. H, cerci. Scale bars. A, E = 0.1 mm; B, C, H = 0.05 mm; D, F, G = 0.025 mm.

Description. Female (Figs. 5 and 6A). Total length = 1.18 mm. *Head*. Compound eyes separated mid-dorsally by a distance of 3–4 ommatidia, single vertex seta present (Fig. 6B). Antenna with 13 separated flagellomeres gradually increasing in length towards the apex (Fig. 6C); basal flagellomeres with sensilla trichoidea. Mouthparts moderately elongated; mouthpart length/length of fifth tarsomere of foreleg = 2.8. Palpus 5-segmented; palpal segment 3 greatly swollen and laterally flattened, ovoidal in lateral view; palpal segment 4 small, much shorter than palpal segment 5 (Fig. 6D). *Thorax*. Scutum with elongated setae; scutellum not visible in dorsal view. *Wing*. Length = 0.91 mm, costal ratio = 0.97. Stylised wing shape (Fig. 6E). Wing membrane without macrotrichia, microtrichia distinct. C distinctly extending beyond R_3. Two well-developed radial cells, very elongated; second radial cell slightly longer than the first one. Transverse vein r-m oblique, not subperpendicular to C. M petiolate. Vein M_2 basally absent. *Legs*. Slender. Foreleg with two thick tibial spurs (Fig. 6F); midleg possibly with slender apical spur. Thick, paired spines at apex of tarsomeres 1–4 conspicuous only in mid- and hindlegs. Tarsal ratio of foreleg = 2.6, hindleg = 1.3, foreleg/hindleg = 2. Claws short, simple, similar in all legs (Fig. 6G). *Genitalia*. Cerci very short (Fig. 6H).

Remarks. The specimen ES-07-17 can be placed in the genus *Archiaustroconops* in that it shows: (a) two well-developed radial cells, (b) an oblique tranverse vein r-m, and (c) a foreleg/hindleg tarsal ratio > 1.4 (Borkent, 2000a).

Archiaustroconops borkenti sp. nov. shares most of its features with *A. alavensis* and *A. szadziewskii*. Unlike the other *Archiaustroconops* species, all three have a 5-segmented palpus where the palpal segment 4 is much shorter than segment 5, and equal and simple tarsal claws (not basally toothed). *A. borkenti* displays a wing morphology similar to *A. szadziewskii* (high costal ratio, first radial cell long, and Cu-A bifurcating distally; Borkent, 2000a), but its eyes are separated mid-dorsally and its palpal segment 3 is greatly swollen and laterally flattened, as occurs in *A. alavensis* (Szadziewski and Arillo, 1998; Szadziewski and Poinar, 2005) (eyes broadly abutting dorsally and palpal segment 3 slightly swollen in *A. szadziewskii*).

A recent examination of the ceratopogonid collection from the "Museo de Ciencias Naturales de Álava" revealed one specimen from Peñacerrada I amber with antennal and wing characters which coincided with those of *A. borkenti*.

Genus *Austroconops* Wirth and Lee, 1958

Type species. *Austroconops mcmillani* Wirth and Lee, 1958.

Range and locality. Early Cretaceous (late Barremian–Aptian) to Recent. *Austroconops fossilis* Szadziewski, 1996, *A. gondwanicus* Szadziewski, 1996, *A. gladius* Borkent, 2000 and *A. megaspinus* Borkent, 2000 from late Barremian–Aptian Lebanese amber; *Austroconops asiaticus* Szadziewski, 2004 from late Albian–Cenomanian Burmese (Myanmar) amber; *A. borkenti* Szadziewski and Schlüter, 1992 from Cenomanian Bezonnais amber (NW France); *Austroconops sibiricus* Szadziewski, 1996 from Coniacian–Santonian Yantardakh amber (Taimyr, northern Russia); *A. mcmillani* Wirth and Lee, 1958 and *A. annettae* Borkent, 2004 from Western Australia.

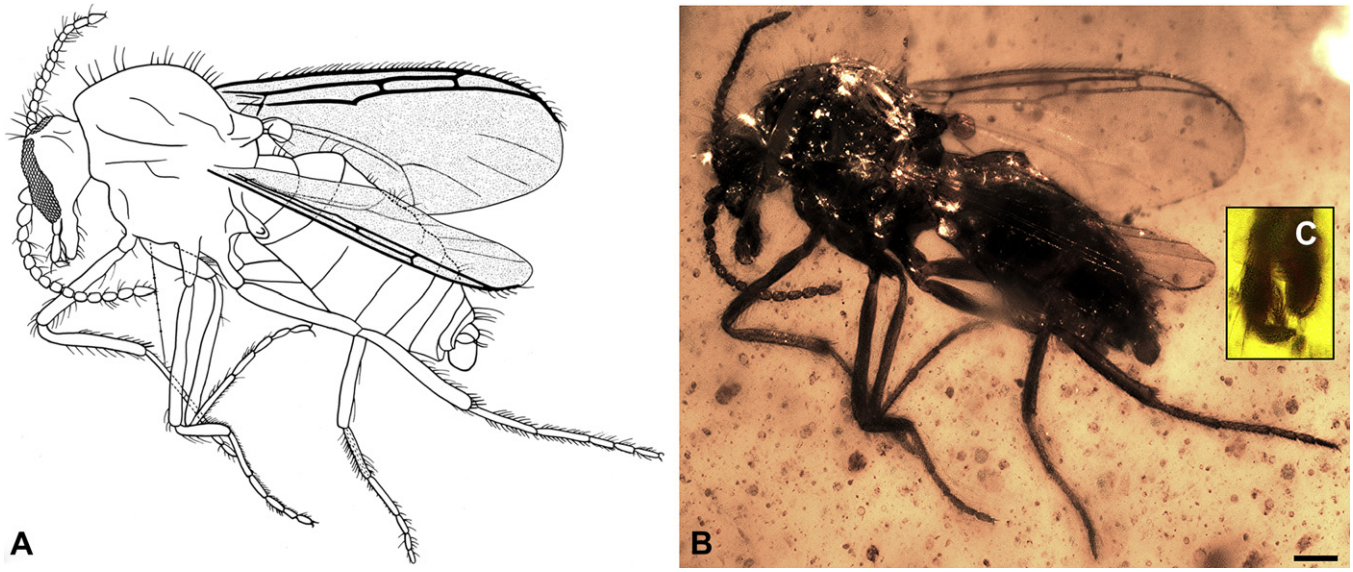

Fig. 7. *Austroconops* sp., CES-017.1. A, camera lucida drawing. B, photograph. C. detail of the mouthparts, showing the left palpal segments 3 and 4 + 5 in the foreground. Scale bar = 0.1 mm.

Austroconops sp.

Material. Two females, CES-008 and CES-017.1. The latter specimen is in a reconstructed stalactite-shaped amber piece, together with a platygastrid (Hymenoptera) as syninclusion (CES-017.2). It is well-preserved, though the right midleg is apparently missing. A gas bubble at the end of the abdomen, and a thread of a spider's web adhering to the thorax and the left midleg can be seen. CES-008 has been affected by a tangential fracture of the amber piece, having lost a part of the cephalic region. As a result, neither antennae are preserved, but one palpus and the distal half of the mouthparts can be seen in detail.

Description. Female (Fig. 7). Total length = 0.99–1.20 mm. *Head*. Compound eyes probably separated mid-dorsally by a short distance. Single vertex seta not evident. Antenna with 13 separate flagellomeres; flagellomeres 9–13 slightly more elongated than those preceding them; last flagellomere subconical in shape. Mouthparts moderately elongated; mouthpart length/length of fifth tarsomere of foreleg = 2.6–2.8. Palpus 4-segmented; segment 3 slender, slightly swollen, ca. 3 times as long as its greatest width; segment 4 + 5 ca. 2.5 times as long as its greatest width; segments 3/4 + 5 = 1.6–1.8 (Fig. 7C). *Thorax*. Scutum setose. Scutellum with rounded apex. *Wing*. Length = 0.73–0.80 mm, costal ratio = 0.99. Single row of macrotrichia at dorsal margins of R and C. Wing membrane without macrotrichia, microtrichia distinct. Subcosta (Sc) absent. C extending beyond apex of vein R_3. Two well-developed radial cells present, elongated, subequal in length. Transverse vein r-m long, parallel to R_1. M petiolate. Veins M_1 and M_2 basally absent, completely absent in specimen CES-008. *Legs*. Slender. Pair of thick setae not visible on fore- and midleg trochanter. Foreleg tibiae with two slender, short tibial spurs; midleg tibial spur not present; hindleg tibiae with single transverse row of apical spines (= tibial comb). Hindleg first tarsomere with scattered setae. Thick, paired spines at apex of tarsomeres 1–4 poorly conspicuous. Tarsal ratio of foreleg = 2–2.6, hindleg = 1.3, foreleg/hindleg = 1.5–2. Claws simple, slender, similar in all legs. *Genitalia*. Cerci short, rounded.

Remarks. Both specimens can be placed in the genus *Austroconops* in accordance with two well-developed radial cells and the very diagnostic vein r-m parallel to R_1 (Borkent, 2000a). A combination of important characters supports the exclusion of the two El Soplao specimens from most of the species within the genus: (a) a foreleg tibial spur not especially enlarged, (b) a C almost reaching the total wing length (costal ratio almost 1) and (c) two radial cells subequal in length. In fact, the two specimens strongly resemble *A. borkenti* Szadziewski and Schlüter, 1992, mainly in the following characters: (a) palpus 4-segmented, with a palpal segment 3 slender in shape (ca. 3 times as long as its greatest width) and 1.6–1.8 longer than the segment 4 + 5 (Szadziewski and Schlüter, 1992, Fig. 21), (b) flagellomeres 9–13 only slightly more elongated than those preceding them (visible only in CES-017.1), and (c) simple claws, not basally toothed (Szadziewski and Schlüter, 1992). *A. borkenti* was described as a single female from Cenomanian Bezonnais amber (north-west France), which is partially preserved, lacking the distal wing half and some leg segments (Szadziewski and Schlüter, 1992). Its preserved proximal wing portion seems to show an elongated first radial cell (Szadziewski and Schlüter, 1992, Fig. 24), which within the known diversity of the genus would mean that both radial cells are subequal in length or, at least, the second is not much more elongated than the first. Two differences have been noted between the two *Austroconops* sp. specimens from El Soplao and the *A. borkenti* holotype: the lack of Sc and a palpal segment 4 + 5 slightly less elongated.

We have recently re-examined the ceratopogonid collection from Peñacerrada I amber in the "Museo de Ciencias Naturales de Álava". *Austroconops* proved to be very abundant, including two well-preserved male specimens from more than 30 inclusions belonging to this genus. The female specimens from Álava appear to show very constant antennal, palpal and wing characters, similar to those of *A. borkenti*. We prefer not to relate the specimens from El Soplao to *A. borkenti* until this abundant material has been studied further.

On the other hand, although the antennae of CES-008 are not preserved, the other diagnostic characters such as the palpal shape and the simple claws are sufficient to relate it to CES-017.1. In addition, there are some minor differences between the two El Soplao specimens that should be noted. Besides a certain difference in size and foreleg tarsal ratios, whereas CES-017.1 lacks the basal part of M_1 and M_2, CES-008 entirely lacks these two veins. Moreover, CES-017.1 has a palpus somewhat more gracile than CES-008. Lastly, only CES-017.1 presents an r-m vein where the most

proximal stretch is markedly transversal, and then drastically changes its angle, rapidly reaching a continuous, nearly parallel trajectory to R_1. This exact r-m morphology has previously been drawn in *A. gladius* and *A. fossilis* females (Borkent, 2000a, Fig. 12h, 13c), and seems to be absent in the *A. borkenti* holotype. It is significant to note that the vein r-m shows a certain graduation of parallelness within the genus. This fact could be interpreted as an intermediate state between a transverse r-m, present in supposedly more ancestral forms, and the parallel one characteristic of *Austroconops*.

Subfamily: Forcipomyiinae Lenz, 1934
Genus *Atriculicoides* Remm, 1976

Type species. *Atriculicoides macrophthalmus* Remm, 1976.

Range and locality. Early–Late Cretaceous (late Albian–Campanian). *Atriculicoides swinhoei* (Cockerell, 1919) from late Albian–Cenomanian Burmese (Myanmar) amber; *Atriculicoides cenomanensis* Szadziewski and Schlüter, 1992, and *A. incompletus* Szadziewski and Schlüter, 1992 from Cenomanian French amber; *Atriculicoides macrophthalmus* Remm, 1976, *A. dasyheleis* Szadziewski, 1996, *A. sibiricus* Szadziewski, 1996, and *A. taimyricus* Szadziewski, 1996 from Coniacian–Santonian Yantardakh amber (Taimyr, Russia); *Atriculicoides globosus* (Boesel, 1937) from Campanian Canadian amber.

Atriculicoides szadziewskii sp. nov.

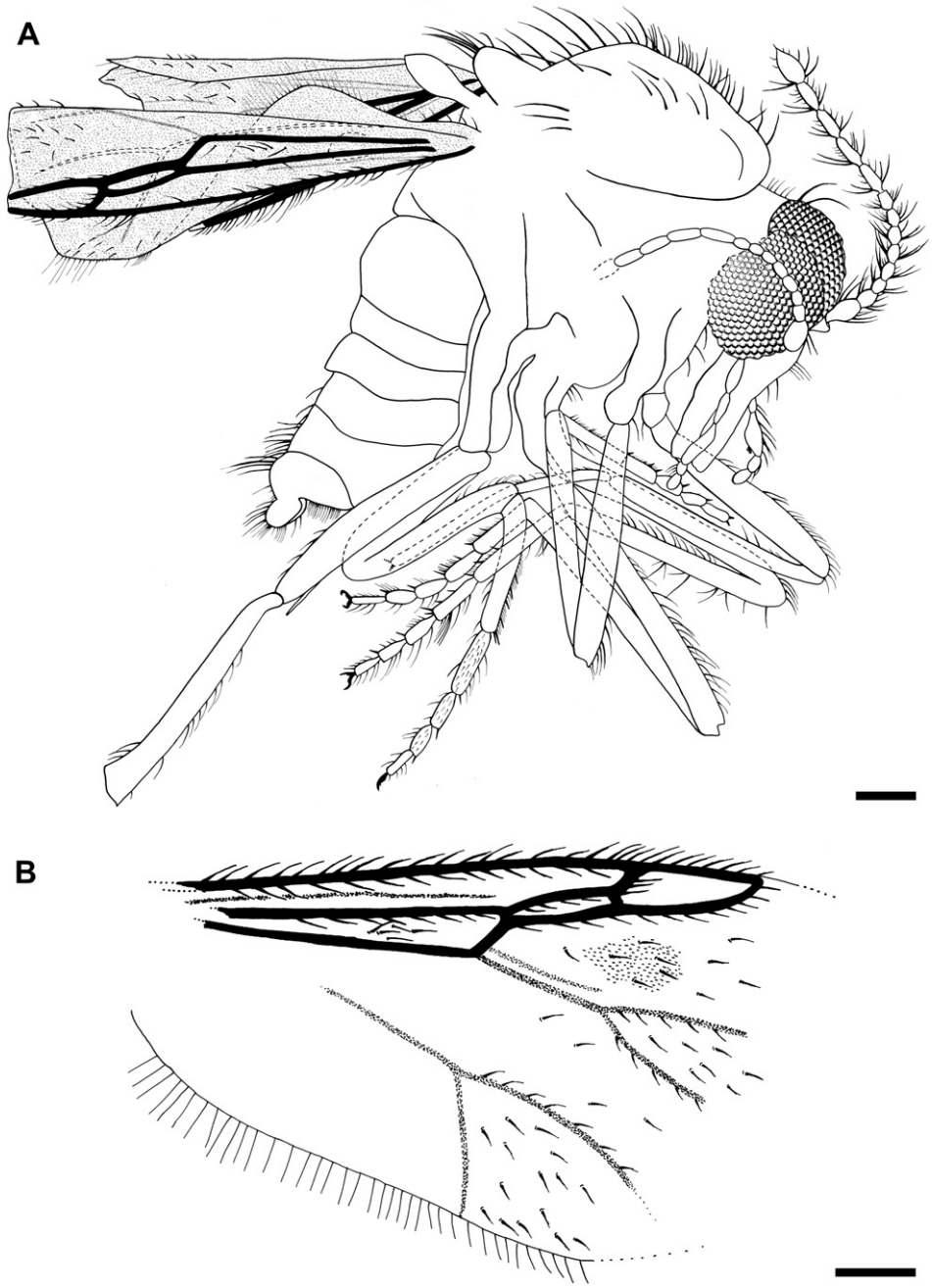

Fig. 8. Camera lucida drawings of *Atriculicoides szadziewskii* sp. nov., holotype ES-07-12. A, lateral habitus. B, wing reconstruction based on the visible preserved parts of both wings. The total wing width has been estimated. Scale bars = 0.1 mm.

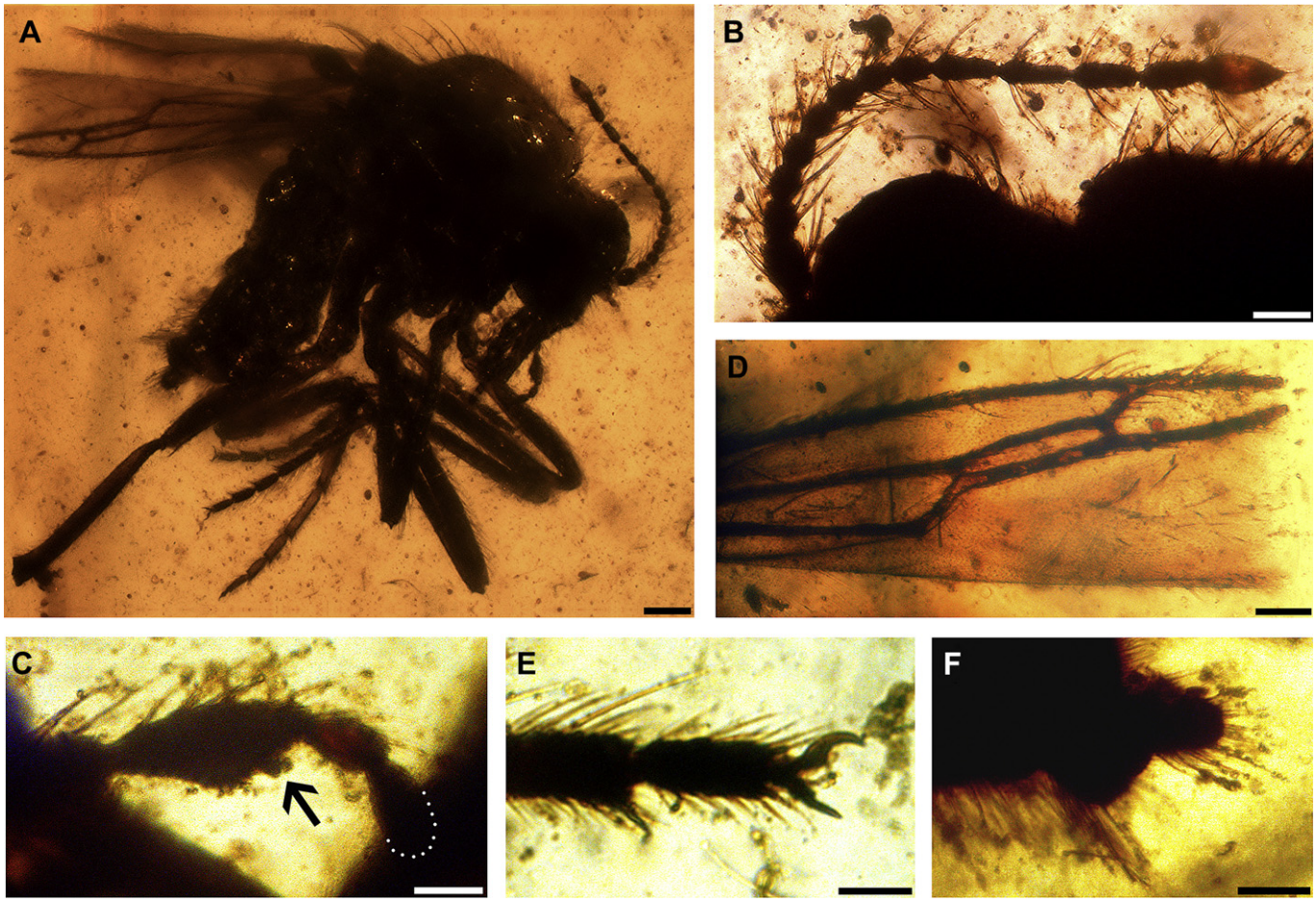

Fig. 9. *Atriculicoides szadziewskii* sp. nov., holotype ES-07-12. A, lateral habitus. B, flagellum of the left antenna. C, left palpus. Arrow points to possible capitate sensilla in the distal part of the palpal segment 3. Limits of the palpal segment 5 have been partially drawn. D, preserved portion of the right wing. E, tarsal claws of right midleg. F, cerci. Scale bars. A = 0.1 mm; B, D, F = 0.05 mm; C, E = 0.025 mm.

Material. Single female, ES-07-12, in a preparation containing fragments of a leg and wings of a cockroach (ES-07-13) as syninclusions. The specimen was found together with three more syninclusions, a beetle indet. (ES-07-14), and two platygastrid wasps (ES-07-15, ES-07-16). The specimen is well-preserved, although both wings are folded and unpreserved around the union between C and R_3 (left wing shows this contact, right wing does not). The distal part of the right antenna is poorly conspicuous due to its proximity to the body. The right hindleg tarsus is not preserved. A spider's web thread adheres to the C of the right wing and the right hindleg tibia.

Derivation of name. The species is named in honour of Dr Ryszard Szadziewski, in recognition of his valuable dedication to the study of biting midges.

Diagnosis. *Male*. Unknown. *Female*. Mouthparts elongated; 5-segmented palpus with segment 3 swollen at mid length and segment 4 slightly shorter than segment 5, both elongately ovate; wing with macrotrichia only sparsely covering the basal radial cell plus the distal half of the wing membrane; cubital vein bifurcating below the distal part of the basal radial cell.

Description. Female (Figs. 8A and 9A). Total length = 1.31 mm. *Head*. Compound eyes broadly abutting mid-dorsally. Single vertex seta not visible. Antenna with 13 separated flagellomeres; flagellomeres 9–13 more elongated than those preceding them; last flagellomere especially elongated and widened in the shape of a paintbrush-like club (could be an artefact; see remarks), with a single seta at the pointed apex (Fig. 9B). Clypeus convex. Mouthparts elongated; mouthpart length/length of fifth tarsomere of foreleg = 5.5. Palpus 5-segmented; segment 3 stout, swollen at mid length, possibly with capitate sensilla in an apparently small sensory pit at apex (Fig. 9C); segment 4 slightly shorter than segment 5, both elongately ovate and exceeding mouthpart length; segments 3/4 = 3.2. *Thorax*. Scutum very raised and setose, with some long thick setae in the posterior area. Scutellum rounded, with a few long setae at the margin. *Wing*. Total length and costal ratio unknown. C and R with macrotrichia. M with single row of macrotrichia. Macrotrichia only covering the distal part of the preserved wing membrane plus the basal radial cell (Figs. 8B and 9D); microtrichia distinct. C ending at tip of vein R_3. Two well-developed radial cells present, long, similar in length (second radial cell 1.2 times longer than the first one). Transverse vein r-m oblique, not subperpendicular to C. M petiolate, bifurcating below the base of the second radial cell. Vein M_2 basally absent. Presence of a supplementary evanescent vein that begins at r-m base and runs parallel along M root until it bifurcates (conspicuous only in the left wing) (Fig. 8B). Cubital bifurcation below the distal part of the basal radial cell. *Legs.* Moderately slender. Pair of thick setae not visible on fore- and midleg trochanter. Tibial comb not visible. First and second tarsomeres of each leg with scattered, stout spines. Thick, paired spines at apex of tarsomeres 1–4. Tarsal ratio of

foreleg = 1.7, hindleg = 1.8, foreleg/hindleg = 0.94. Claws short, simple, similar in all legs, angularly widened at their base (Fig. 9E). *Genitalia*. Cerci short, rounded, highly setose (Fig. 9F).

Remarks. The specimen ES-07-12 is placed within the genus *Atriculicoides* by (a) eyes broadly abutting mid-dorsally, (b) two well-developed radial cells, (c) an oblique tranverse vein r-m, and (d) the presence of macrotrichia on the wing membrane. An especially enlarged terminal flagellomere is also common for this genus. Macrotrichia covering only the distal half of the wing have been reported for males of *A. cenomanensis* and *A. macrophthalmus* (Remm, 1976; Szadziewski and Schlüter, 1992), although the presence of macrotrichia in the basal radial cell, as in *A. szadziewskii* sp. nov., has hitherto been noted only in those wing membranes fully covered by macrotrichia (Remm, 1976; Borkent, 1995; Szadziewski, 1996, 2004).

Within *Atriculicoides*, the last flagellomere tends to be enlarged in relation to those preceding it in length and thickness. In fact, when Remm (1976, p. 345) established the etymology of this genus he noted the coincidence of this character, described as a "small club at the apex of the antenna", with *Culicoides* Latreille, 1809. Subsequently, this character has been observed to a different degree in most of the described *Atriculicoides* species. Although both final flagellomeres of *A. szadziewskii* sp. nov. are undoubtely enlarged, that of the left antenna shows a distinctive paintbrush-like morphology (Fig. 9B). Nevertheless, this specific morphology could reflect an artefact of preservation since the last flagellomere of the right antenna, though distinctly swollen, appears more cylindrical, but is poorly visible because it is very close to the body. As this character is not clearly resolved, it has been excluded from the diagnosis.

6. Palaeoecological remarks

The genera *Leptoconops* Skuse, 1889, and *Austroconops* Wirth and Lee, 1958, are the only living representatives of the ancient Early Cretaceous lineages of the Ceratopogonidae. Whereas nowadays ca. 140 *Leptoconops* species show a pantropical distribution and the only two known recent species of *Austroconops* are restricted to Western Australia, during the Late Cretaceous both genera were widely distributed in the Northern Hemisphere and Eurasia, respectively (see Szadziewski, 2008, Fig. 6, 7B). Larval stages of the two extant genera today burrow mostly within moist soils, often on or near the sea-shore, in beach sands or coastal marsh muds (Downes and Wirth, 1981; Borkent, 2001; Borkent and Craig, 2004). According to this particular larval habitat, it has been reported that the presence of *Leptoconops* sp. in the Cretaceous amber record reflects the proximity of amber producing trees to the sea-shore (Szadziewski, 2004), in keeping with the delta-estuarine scenario generally displayed by the main Cretaceous amber deposits (Alonso et al., 2000; Cruickshank and Ko, 2003; Perrichot et al., 2007). The genera *Leptoconops* and *Austroconops* have always been found together, sometimes as syninclusions, and also together with the genera *Archiaustroconops* and *Protoculicoides*, in the main Early Cretaceous ambers: late Barremian–Aptian of Lebanon (Borkent, 2000a, b, 2001), early Albian of Spain (Szadziewski and Arillo, 1998, 2003), and late Albian–Cenomanian of Myanmar (Szadziewski, 2004; Szadziewski and Poinar, 2005). Therefore, although a future find of the genus *Leptoconops* in El Soplao is highly probable, the mere presence of the genus *Austroconops* enables us to interpret that resin source forests would have developed close to marine coasts in El Soplao as well. This is also suggested by the sedimentological, taphonomical, and other palaeontological data (Najarro et al., 2009, 2010).

On the other hand, females of both genera are today diurnal blood feeders of mammals, birds, and reptiles (Downes and Wirth, 1981; Borkent, 2001; Borkent and Craig, 2004). Blood provides the high protein supply necessary to promote egg development in females, which in derived non-haematophagous biting midges can be achieved by other protein-rich meals such as insect haemolymph or pollen (Grimaldi and Engel, 2005). However, whereas the plesiotypic condition of haematophagy within Culicomorpha is still not clear (Lukashevich and Mostovski, 2003), cladistic analyses indicate that it would have been well established in the basal lineages of Ceratopogonidae (Borkent, 1995; Szadziewski, 1996). Furthermore, despite the fact that finely toothed mandibles and lacinia with retrorse teeth were not observed in the new fossil ceratopogonid taxa – a typical vertebrate blood-feeding indicator reported for some species of *Atriculicoides* and *Protoculicoides* (Borkent, 1995, 2000a, b) – none of them bears enlarged or toothed tarsal claws, an absence strongly correlated with vertebrate blood-feeding in Ceratopogonidae (Szadziewski and Schlüter, 1992). It should be noted that mouthpart length is not a deciding factor for ceratopogonid haematophagous condition since extant blood-feeding Leptoconopinae representatives often show short or very short mouthparts (ibid.). Thus, haematophagy can be assumed not only for the two specimens assigned to *Austroconops* sp. but also for the rest of the El Soplao biting midges.

Moreover, it is highly plausible that haematophagous biting midges would have fed on dinosaur blood during the Cretaceous Period. Dinosaurs would have been preferentially bitten on exposed, heavily vascularised areas, such as the eyelids, as indicated by Borkent (1995). This author reviewed several studies carried out on extant *Culicoides* species, demonstrating the indirect correlation between number of CO_2 host-tracking sensilla in palpal segment 3 and host size, a general tendency also existing in other culicomorphan families. Thus, he concluded that host size of Cretaceous *Culicoides* would have coincided with that of dinosaurs.

Furthermore, as supported in some fossil evidence in amber, it has been hypothesised that the role played by haematophagous biting midges today, acting as vectors of vertebrate pathogens such viruses, nematodes, and protozoa, was also present in the first stages of their evolutionary history during the Early Cretaceous (Poinar and Poinar, 2005; Poinar, 2008), although the majority of these reports should be viewed with caution.

7. Conclusions

Previous reports have demonstrated that the genera *Archiaustroconops*, *Atriculicoides*, *Austroconops* and *Protoculicoides* had an expanded palaeogeographical distribution throughout the Northern Hemisphere during, at least, the Early Cretaceous. Our new record of the genus *Lebanoculicoides* also reveals a relatively wide palaeogeographic distribution of what is thought to be the basalmost genus of the Ceratopogonidae. The find of *A. szadziewskii* sp. nov. represents the oldest record for this genus to date. The co-occurrence of *P. skalskii* in Peñacerrada I, San Just, and now in El Soplao, provides relevant palaeoentomological evidence in support of a similar palaeoecology for these three Spanish amber localities.

The presence of biting midges in El Soplao amber, although not surprising, has great palaeoenvironmental significance, since it suggests the proximity of resin producing forests to marine coastal areas during the early–middle Albian. In addition, the five taxa discussed here would have fed on vertebrate blood, possibly acting as vectors and therefore spreading pathogens. Indeed, dinosaurs may have been their hosts, as has been indicated previously for other amber records.

The preliminary study of El Soplao amber has already provided a strikingly diverse record of Ceratopogonidae dipterans, suggesting that, as is customary for amber deposits, this group will be one of the most prevalent.

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Anexo I.6

Snakefly diversity in Early Cretaceous amber from Spain (Neuropterida, Raphidioptera)

Diversidad de moscas serpiente en ámbar del Cretácico Inferior de España (Neuropterida, Raphidioptera)

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Resumen:

El ámbar del Albiense de España alberga vigentemente el mayor número y diversidad de moscas serpiente (Raphidioptera) adultas en ámbar. Dentro de Baissopteridae, *Baissoptera*? *cretaceoelectra* sp. n., del yacimiento de Peñacerrada I (Moraza, Burgos), es la primera inclusión en ámbar perteneciente a la familia y descrita del Oeste de Eurasia, y por tanto expande notablemente el rango paleogeográfico de la familia, que se restringía al Cretácico de Brasil y el este de Asia. Dentro de la familia Mesoraphidiidae, se describen *Necroraphidia arcuata* gen. et sp. n. y *Amarantoraphidia ventolina* gen. et sp. n. del yacimiento de El Soplao (Rábago, Cantabria), mientras que se describen *Styporaphidia*? *hispanica* sp. n. y *Alavaraphidia imperterrita* gen. et sp. n. del yacimiento de Peñacerrada I. Además, se reconocen tres morfoespecies a partir de restos fragmentarios. Las combinaciones siguientes se restauran: *Yanoraphidia* gaoi Ren, 1995, stat. rest., *Mesoraphidia durlstonensis* Jepson, Coram & Jarzembowski, 2009, stat. rest. y *Mesoraphidia heteroneura* Ren, 1997, stat. rest. La singularidad de esta rica paleodiversidad podría deberse al aislamiento paleogeográfico del territorio Ibérico y también al predominio de los incendios durante el Cretácico.

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Snakefly diversity in Early Cretaceous amber from Spain (Neuropterida, Raphidioptera)

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Abstract

The Albian amber from Spain presently harbors the greatest number and diversity of amber adult fossil snakeflies (Raphidioptera). Within Baissopteridae, *Baissoptera*? *cretaceoelectra* **sp. n.**, from the Peñacerrada I outcrop (Moraza, Burgos), is the first amber inclusion belonging to the family and described from western Eurasia, thus substantially expanding the paleogeographical range of the family formerly known from the Cretaceous of Brazil and eastern Asia. Within the family Mesoraphidiidae, *Necroraphidia arcuata* **gen. et sp. n.** and *Amarantoraphidia ventolina* **gen. et sp. n.** are described from the El Soplao outcrop (Rábago, Cantabria), whereas *Styporaphidia*? *hispanica* **sp. n.** and *Alavaraphidia imperterrita* **gen. et sp. n.** are described from Peñacerrada I. In addition, three morphospecies are recognized from fragmentary remains. The following combinations are restored: *Yanoraphidia* gaoi Ren, 1995, **stat. rest.**, *Mesoraphidia durlstonensis* Jepson, Coram and Jarzembowski, 2009, **stat. rest.**, and *Mesoraphidia heteroneura* Ren, 1997, **stat. rest.** The singularity of this rich paleodiversity could be due to the paleogeographic isolation of the Iberian territory and also the prevalence of wildfires during the Cretaceous.

Keywords
Holometabola, taxonomy, paleontology, paleogeography, Mesozoic, Albian

Introduction

Raphidioptera (snakeflies) are regarded as one of the most primitive lineages of holometabolous insects, their fossil record dating back to the Early Jurassic (Grimaldi and Engel 2005). There is consensus that Raphidioptera forms a distinct clade together with Megaloptera and Neuroptera, the superorder Neuropterida. However, there is controversy whether Raphidioptera is sister to Megaloptera or to [Megaloptera + Neuroptera] (see Haring et al. 2011). Nowadays, the active, predatory larvae of snakeflies are long-lived, with a high number of instars and distinctive hibernating periods, living under the bark of trees and shrubs or in soil detritus; moreover, their pupation needs a period of cold to break diapause, and the pupae are exarate and active, a plesiotypic condition within Holometabola (Aspöck 2002). Adults are arboreal and also predatory, but short-lived (ibid.), exhibiting a prognathous head, a long pronotum, and a long ovipositor in females, features that give them a snake-like appeareance. The extant diversity of the order is relictual, as the Mesozoic diversity of Raphidioptera, as suggested by morphological disparity more-so-than total numbers, was greater than that observed today (e.g., Martynov 1925; Martynova 1961; Ponomarenko 1988, 1993; Oswald 1990; Ren 1997; Engel 2002; Engel et al. 2006; Perrichot and Engel 2007; Jepson and Jarzembowski 2008; Jepson et al. 2009, 2011). Moreover, while the group was once distributed throughout the world and in diverse habitats, today their range is contracted into the cold temperate regions of the Northern Hemisphere. The fossil record of Raphidioptera is comprised principally of compressions ranging from the Early Jurassic through the Miocene (Engel 2002). Snakefly inclusions in amber are far more uncommon (e.g., Carpenter 1956; Engel 1995; Aspöck and Aspöck 2004), particularly those in Cretaceous resins (Grimaldi 2000; Engel 2002; Perrichot and Engel 2007; Engel and Grimaldi 2008; Pérez-de la Fuente et al. 2010; Bechly and Wolf-Schwenninger 2011).

Raphidioptera currently comprises six families, i.e., four extinct families, Mesoraphidiidae Martynov, 1925 (Late Jurassic – Late Cretaceous), Baissopteridae Martynova, 1961 (Late Jurassic – Early Cretaceous), Priscaenigmatidae Engel, 2002 (Early Jurassic; classified into its own suborder and considered the most primitive raphidiopterans), and Metaraphidiidae Bechly and Wolf-Schwenninger, 2011 (Early Jurassic); and two extant families that date back to the Eocene, Raphidiidae Latreille, 1810 and Inocelliidae Navás, 1913 (Grimaldi and Engel 2005), with ca. 210 and ca. 30 extant species respectively (Haring et al. 2011). The extinct family Baissopteridae currently comprises about 20 species distributed in five genera (Table 1). The family is considered to represent a plesiomorphic condition within Raphidioptera owing to the dense crossvenation of its representatives (Engel 2002), and it could be paraphyletic (Willmann 1994; Bechly and Wolf-Schwenninger 2011). To date, baissopterids have been exclusively recorded from Cretaceous localities, hitherto restricted to Brazil

Table 1. Currently recognized genera classified within the extinct families Baissopteridae and Mesoraphidiidae.

Family Baissopteridae Martynova, 1961
Genus *Austroraphidia* Willmann, 1994
Genus *Baissoptera* Martynova, 1961
Genus *Cretoraphidia* Ponomarenko, 1993
Genus *Cretoraphidiopsis* Engel, 2002
Genus *Lugala* Willmann, 1994
Family Mesoraphidiidae Martynov, 1925
Genus *Alavaraphidia* Pérez-de la Fuente, Peñalver, Delclòs & Engel, gen. n.
Genus *Alloraphidia* Carpenter, 1967
Genus *Amarantoraphidia* Pérez-de la Fuente, Peñalver, Delclòs & Engel, gen. n.
Genus *Archeraphidia* Ponomarenko, 1988
Genus *Baisoraphidia* Ponomarenko, 1993
Genus *Cantabroraphidia* Pérez-de la Fuente, Nel, Peñalver & Delclòs, 2010
§ Genus *Cretinocellia* Ponomarenko, 1988
Genus *Grimaldiraphidia* Bechly and Wolf-Schwenninger, 2011
Genus *Huaxiaraphidia* Hong, 1992
Genus *Iberoraphidia* Jepson, Ansorge & Jarzembowski, 2011
Genus *Jilinoraphidia* Hong and Chang, 1989
Genus *Kezuoraphidia* Willmann, 1994
Genus *Lebanoraphidia* Bechly & Wolf-Schwenninger, 2011
Genus *Mesoraphidia* Martynov, 1925
Genus *Nanoraphidia* Engel, 2002
Genus *Necroraphidia* Pérez-de la Fuente, Peñalver, Delclòs & Engel, gen. n.
Genus *Ororaphidia* Engel & Ren, 2008
Genus *Pararaphidia* Willmann, 1994
Genus *Proraphidia* Martynova, 1947
Genus *Siboptera* Ponomarenko, 1993
Genus *Sinoraphidia* Hong, 1982
Genus *Styporaphidia* Engel & Ren, 2008
Genus *Xuraphidia* Hong, 1992
Genus *Yanoraphidia* Ren, 1995

§ Recently transferred from Baissopteridae by Bechly and Wolf-Schwenninger (2011).

and eastern Eurasia (China, Mongolia, and Russia) (Fig. 1). The extinct family Mesoraphidiidae currently comprises about 60 species classified in 24 genera (Table 1). For an up-to-date view of the family, there is a catalog provided by Engel (2002), supplemented by Engel and Ren (2008), Jepson and Jarzembowski (2008), Jepson et al. (2009, 2011), Pérez-de la Fuente et al. (2010), and Bechly and Wolf-Schwenninger (2011). Hitherto, less than 10% of this diversity is described from amber inclusions and thus from specimens potentially more informative (Table 2). Mesoraphidiidae has been recorded from several Jurassic and Cretaceous localities primarily of the Northern Hemisphere (see Pérez-de la Fuente et al. 2010: fig. 1, supplemented by the species described from new localities by Jepson et al. 2011, Bechly and Wolf-Schwenninger 2011, and the present contribution).

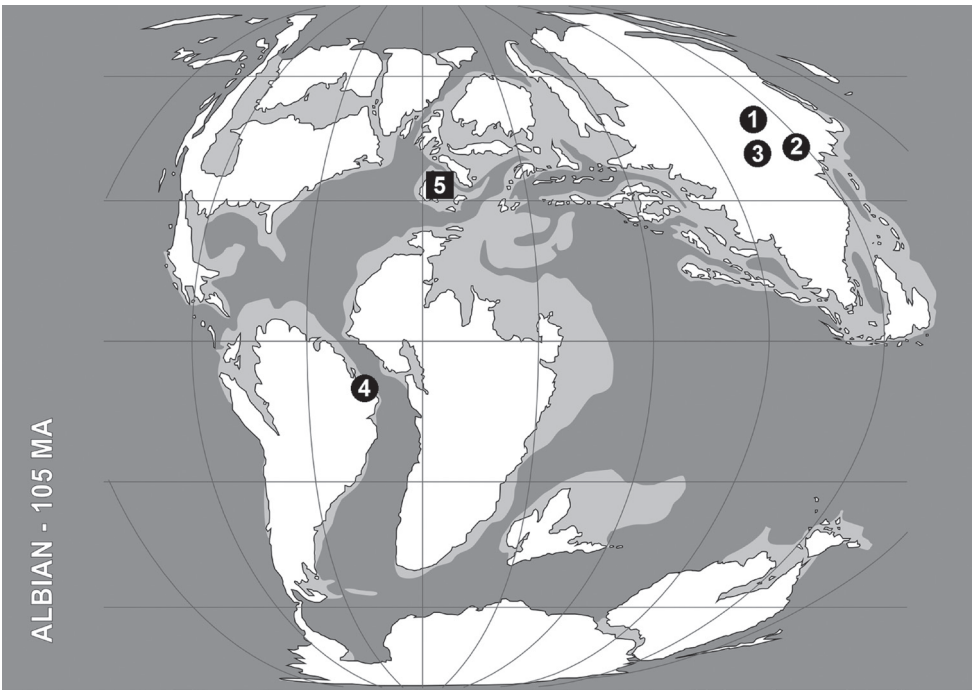

Figure 1. Distribution of the Early Cretaceous snakeflies currently classified within the Baissopteridae. The paleogeographic map (redrawn from Blakey 2008) corresponds to middle Albian (ca. 105 Ma). Data summarized in Engel (2002) and complemented with Jepson et al. (2011) and this paper. Circles correspond to compression localities, whereas the square represents the single amber locality in which baissopterids have been described up to date. Localities appear in chronological order after the ages summarized in Grimaldi and Engel (2005), although the age of the localities from Eastern Asia are considered generically as Early Cretaceous. Note that *Cretinocellia cellulosa* Ponomarenko, 1988 was transferred to Mesoraphidiidae s.s. by Bechly and Wolf-Schwenninger (2011) **1** Baissa, Buryat Republic, Russia (Neocomian, Valanginian). *Baissoptera cellulosa* Ponomarenko, 1993, *B. elongata* Ponomarenko, 1993, *B. kolosnitsynae* Martynova, 1961, *B. martinsoni* Martynova, 1961, *B. minima* Ponomarenko, 1993, and *B. sibirica* Ponomarenko, 1993; *Cretoraphidia certa* Ponomarenko, 1993, *C. macrocella* Ponomarenko, 1993, *C. magna* Ponomarenko, 1993, and *C. reticulata* Ponomarenko, 1993 **2** Liaoning, China (Neocomian: Hauterivian?). *Baissoptera euneura* Ren, 1997, *B. grandis* Ren in Ren et al., 1995, and *B. liaoningensis* Ren, 1994. **3** Bon-Tsagan, Mongolia (Barremian). *Cretoraphidiopsis bontsaganensis* (Ponomarenko, 1988); *Lugala longissima* (Ponomarenko, 1988) **4** Ceará, Brazil (Aptian). *Austroraphidia brasiliensis* (Nel, Séméria, and Martins-Neto, 1990); *Baissoptera brasiliensis* Oswald, 1990, *B. pulchra* (Martins-Neto & Nel, 1992), and *B. lisae* Jepson, Ansorge and Jarzembowski, 2011 **5** Peñacerrada I (=Moraza) amber, Burgos, Spain (Albian). *Baissoptera*? *cretaceoelectra* sp. n.

The recent discovery of a significant paleodiversity of snakeflies in Spanish amber stimulated the present work. Herein we describe this diversity and place it in the context of other Mesozoic snakeflies, highlighting some factors that could explain the uniqueness of this record when compared to other Cretaceous ambers.

Table 2. Cretaceous amber snakeflies (Neuropterida: Raphidioptera).

Age, taxa	Amber locality (country)
Neocomian (Barremian–Aptian)	
Lebanoraphidia nana Bechly and Wolf-Schwenninger, 2011	Jezzine (Lebanon)
Mesoraphidiid larva (in Perrichot and Engel 2007)	Jezzine (Lebanon)
Albian	
Baissoptera? *cretaceoelectra* sp. n.	Peñacerrada I (Spain)
Alavaraphidia imperterrita gen. et sp. n.	Peñacerrada I (Spain)
Styporaphidia? *hispanica* sp. n.	Peñacerrada I (Spain)
Mesoraphidiid gen. et sp. indet. 1 (MCNA 9218)	Peñacerrada I (Spain)
Mesoraphidiid gen. et sp. indet. 3 (MCNA 9316)	Peñacerrada I (Spain)
Cantabroraphidia marcanoi Pérez-de la Fuente et al., 2010	El Soplao (Spain)
Amarantoraphidia ventolina gen. et sp. n.	El Soplao (Spain)
Necroraphidia arcuata gen. et sp. n.	El Soplao (Spain)
Mesoraphidiid gen. et sp. indet. 2 (CES 376)	El Soplao (Spain)
Nanoraphidia electroburmica Engel, 2002	Hukwang (Myanmar)
Mesoraphidiid larva 1 (in Engel 2002)	Hukwang (Myanmar)
Mesoraphidiid larva 2 (in Perrichot and Engel 2007)	Hukwang (Myanmar)
Mesoraphidiid larva 3 (in Perrichot and Engel 2007)	Hukwang (Myanmar)
Late Albian	
Mesoraphidiid larva (in Perrichot and Engel 2007)	Archingeay-Les Nouillers (France)
Turonian	
Grimaldiraphidia luzzii (Grimaldi, 2000)	New Jersey (USA)
Mesoraphidiid larva (in Grimaldi 2000)	New Jersey (USA)
Campanian	
Mesoraphidiid larva (in Engel and Grimaldi 2008)	Grassy Lake (Canada)

Material and methods

Samples designated by the institutional abbreviation CES are housed in the laboratory of the El Soplao Cave, Celis, Cantabria (Spain) encompassing the Institutional Collection from the El Soplao outcrop; whereas those designated as MCNA are housed in the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain. The higher classification followed herein is modified from that of Engel (2002), Perrichot and Engel (2007), and Bechly and Wolf-Schwenninger (2011). We prefer not to recognize subfamilies within Mesoraphidiidae as it is unclear what the monophyletic lineages of this complex truly comprise. Morphological terminology generally follows that of Aspöck et al. (1991). Vein and cell nomenclature is after Engel (2011): the term "radial" is used for cells bounded between R and Rs, "discal" is used for the cell bounded between Rs and MA, "medial" is used for cells bounded between MA and MP, and "discoidal" is reserved for cells bounded anteriorly by MP and posteriorly by MP or CuA (Fig. 9). Also, the number of Rs branches is considered as those that reach the wing margin. Genitalia nomenclature follows that of Aspöck and Aspöck (2008), i.e., the numbers 9, 10 or 11 accompanying abdominal/genitalic structures indicate to which abdominal

segment they allegedly belong; the parameres are considered to be the fused gonocoxites, gonapophyses and gonostyli from the 10th abdominal segment; and the term trichobothria refers to the bristles located in the center of a depressed ring in the cuticle of tergite 10 (+11?) in Neuropterida.

Drawings were prepared with a camera lucida attached to an Olympus BX51 microscope. Photomicrographs were prepared using a Nikon D1x digital camera attached to an Infinity K-2 long-distance microscopic lens. Images were merged using Combine ZP and Helicon Focus 4.2.1 (HeliconSoft Ltd.) softwares. All measurements are in millimeters and were taken using an ocular graticule.

Abbreviations. Veins: A, anal; C, costa; CuA, cubital anterior; CuP, cubital posterior; MA, medial anterior; MP, medial posterior; ptc, pterostigmal crossvein; R, radial; Rs, radial sector; Sc, subcosta. Wing fields (in italics): *dcal*, discal cell; *doi*, discoidal cell; *m*, medial cell; *pt*, pterostigma; *r*, radial cell; *sr*, subradial cell.

Geological setting

The Peñacerrada I (in Moraza, Burgos. 42°40'22"N, 2°42'57"W) and El Soplao (in Rábago, Cantabria. 43°18'20"N, 4°26'50"W) amber-bearing deposits are included within the Basque-Cantabrian Basin (BCB) in the north of the Iberian Peninsula. To the south, the BCB constitutes a thrust sheet on the Cenozoic Duero and Ebro basins, while to the north it extends offshore to the Gulf of Biscay. BCB's oriental limit is in the Pyrenees, and its occidental limit is in the Asturian Paleozoic Massif. The evolution of the BCB during the Late Jurassic-Early Cretaceous was contextualized into a stretching rift setting related with the opening of both the North Atlantic Ocean and the Biscayan Gulf. This regional extension produced a complex distribution of sub-basins and depositional areas, with different sedimentation features between them.

The amber localities are Albian in age, about 110 Mya (Peñalver and Delclòs 2010), and are always associated with coal layers. The amber is included within the Escucha Formation (Peñacerrada I, in the oriental part of the BCB) (Martínez-Torres et al. 2003; Delclòs et al. 2007) and within Las Peñosas Formation (El Soplao, in the occidental part of the BCB) (Najarro et al. 2009, 2010). In Peñacerrada I, the amber is embedded into a siliciclastic unit with organic-rich silts, clays, and coal levels. These levels were deposited in non-marine environments, into interdistributary bays within a deltaic plain, and sometimes were related with channel infillings which drained the surrounding forests. The discontinuous presence of dinoflagellate cysts (Núñez-Betelu 1998) and orbitolinids (Martínez-Torres et al. 2003) suggests a periodical seawater influence. In El Soplao, the amber also occurs in organic-rich silt-claystones which were deposited into interdistributary and coastal bays, or marshes. This deposit is characterized by the presence of some decimetric levels of cuticle-plant remains indicating strong continental influence. They are interbedded with other levels containing brackish or marine gastropods, bivalves, bryozoans, and serpulids (Najarro et al. 2010), some of them fixed on the surfaces of the amber

pieces, and this circumstance suggests a more marine-influenced environment than in the Peñacerrada I outcrop. The Albian amber occurrences in the BCB are coinciding with transitions from maximum regional regressions to deltaic progradations (Martínez-Torres et al. 2003; Najarro et al. 2009).

Paleoecological setting

From Peñacerrada I two different vegetational assemblages were distinguished in palynological analyses (Barrón et al. 2001; Diéguez et al. 2010). One assemblage developed on the alluvial plains and was composed of a mixed conifer forest (chiefly Araucariaceae and Taxodiaceae–Cupressaceae, but also with some Pinaceae, Podocarpaceae and Ginkgoaceae) with an understory characterized by lycopsids and Schizaeaceae. The other assemblage was composed of xeromorphic vegetation that grew on coastal environments, containing Cheirolepidiaceae, Cycadophyta, Gnetophyta, and some arboreal ferns adapted to dry conditions, such as Matoniaceae and Cyatheaceae/Dicksoniaceae/Dipteridaceae. In El Soplao, the area was covered by a mixed forest that grew close to the seaside and was composed by Cheirolepidiaceae, Cupressaceae, and Miroviaceae, with an understory containing pteridophytes, cycads, ginkgoales, and/or bennettitales; swamp and pond areas were occupied by cryptogams and early angiosperms (Najarro et al. 2009, 2010).

Different tree groups have been interpreted as the resin producers. For the oriental area of the BCB (Peñacerrada I), araucariaceans close to the Recent genus *Agathis* were suggested as original producers of the resin (Alonso et al. 2000; Chaler and Grimalt 2005), while in the occidental area (El Soplao), the conifer genus *Frenelopsis*, of the extinct family Cheirolepidiaceae, plus another unidentified plant, were indicated (Menor-Salván et al. 2010; Najarro et al. 2010). The presence in both outcrops of abundant charcoal in the amber-bearing sediments and charcoalified plant fibers embedded into the amber indicates the occurrence of wildfires in the paleoenvironment (Najarro et al. 2010).

Systematic paleontology

Order Raphidioptera Navás, 1916
Suborder Raphidiomorpha Engel, 2002
Family Baissopteridae Martynova, 1961
Genus *Baissoptera* Martynova, 1961

***Baissoptera*? *cretaceoelectra* Pérez-de la Fuente, Peñalver, Delclòs & Engel, sp. n.**
urn:lsid:zoobank.org:act:94EB4ADD-CCC8-46CB-98AF-F2EC4D47BDDC
Figs 2, 3

Holotype. MCNA 12068.4, from Peñacerrada I amber; fore- and hind wing distal fragments. Three associated hymenopterans are preserved as syninclusions.

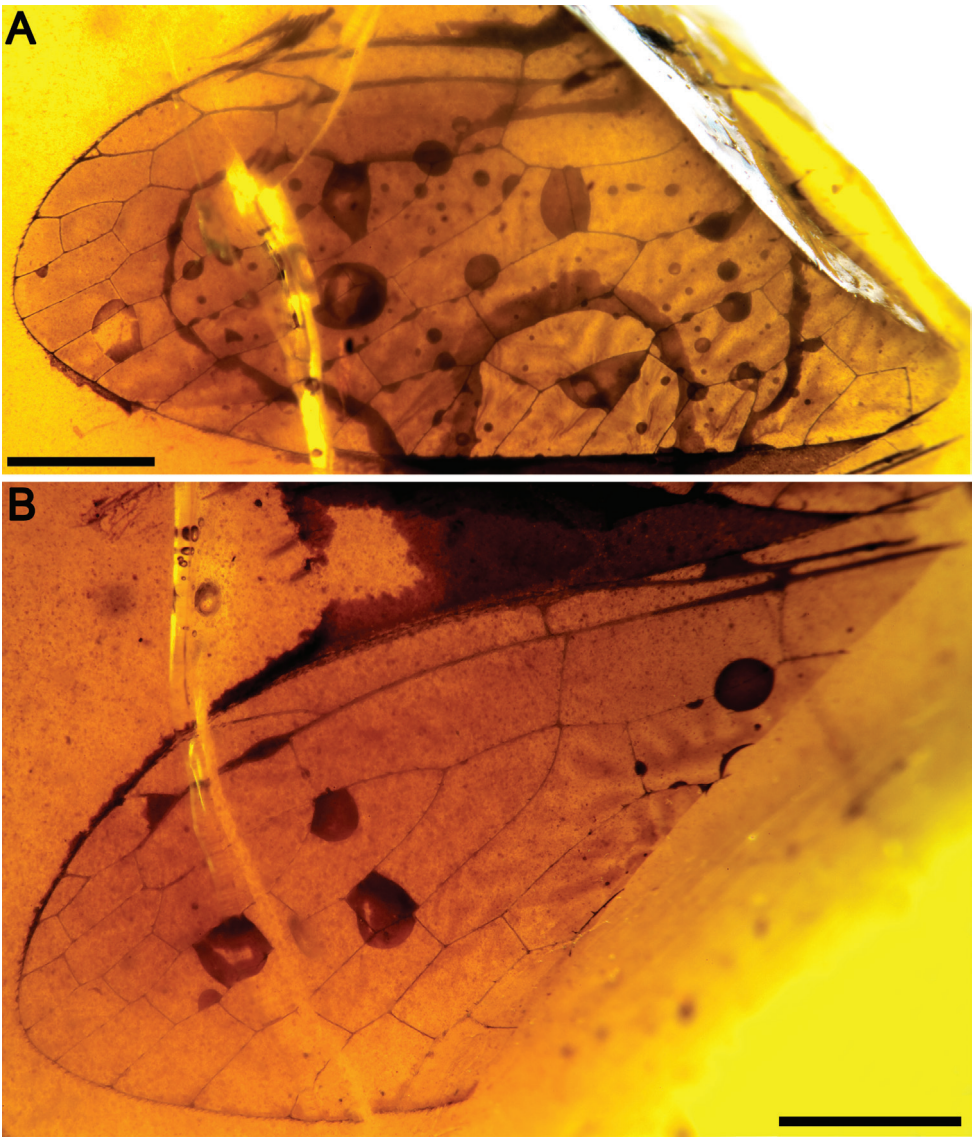

Figure 2. *Baissoptera? cretaceoelectra* sp. n., holotype MCNA 12068.4. **A** forewing **B** hind wing. Scale bars = 1 mm.

Diagnosis. Fore- and hind wing with a relatively long pterostigma with a strongly oblique and slightly sinusoid pterostigmal crossvein placed beyond pterostigmal midlength; fore- and hind wing with one closed radial cell distal to pterostigma; forewing Rs with six branches; forewing with at least eight closed subradial cells.

Description. Sex unknown. Veins with some strong, very short setae preserved, membrane hyaline. *Forewing.* Length of preserved fragment 6.4, maximum width 2.8; wing apex relatively rounded; pterostigma relatively long (2.4 long, length ca. eight

times basal pterostigmal width), slightly widening distally, not conspicuously infumate as preserved; pterostigma with a strongly oblique and slightly sinusoid pterostigmal crossvein placed beyond pterostigmal midlength, basally closed by a crossvein; pterostigma longer than any radial cell; R with two branches beyond pterostigma; at least three radial cells present, one closed radial cell partly distal to pterostigma; Rs with six branches and at least eight closed subradial cells; MA at least with two branches; gradate series very regular, almost following a staircase-like pattern. *Hind wing*. Length of preserved fragment 5.9, maximum width as preserved 2.7; wing apex more pointed than in forewing; costal field distinctly narrower than in forewing; one c-sc crossvein preserved; pterostigma relatively long (2.5 long, length ca. 10 times basal pterostigmal width), slightly widening distally, not conspicuously infumate as preserved, starting 0.5 (twice pterostigmal basal width) beyond termination of Sc; pterostigma with a strongly oblique and slightly sinusoid pterostigmal crossvein placed beyond pterostigmal midlength, basally closed by a crossvein; pterostigma longer than any radial cell; R with two branches beyond pterostigma; at least five radial cells present, one small closed radial cell distal to pterostigma; Rs with five branches and at least seven closed subradial cells; MA at least with two branches; gradate series very regular, almost following a staircase-like pattern.

Etymology. The specific epithet is a combination of the Greek words *cretaceus* (taken from the period name, although specifically meaning "chalky") and *elektron*, meaning "amber".

Comments. Within the current taxonomic framework, the numerous crossveins of MCNA 12068.4 are indicative of placement in the Baissopteridae. Unfortunately, neither base of the wing is preserved, thus important characters such as the maximum width of the costal field, the pattern of distribution of c-sc crossveins (= costal crossveins), the separation between M and CuA in the forewing, and the shape of the basal piece of MA, are unknown. Also, the infumation of the pterostigma is not evident in the holotype, but it is uncertain if this could have been caused by taphonomical processes and is, therefore, not used as a diagnostic character although if the absence of infumation is true of the species in life, then it would represent a remarkable difference from all other described baissopterids. Fortunately, the pterostigma can be delimited thanks to the relative parallelness of C and R (R tends to conspicuously change its slope beyond the pterostigma in the other baissopterids) and also the greater thickness of both veins.

The specimen is tentatively classified within the genus *Baissoptera* as it has the pterostigmal crossvein most similar to the diversity found within this genus. Today just two of the 12 species currently classified within the genus *Baissoptera*, i.e., *B. brasiliensis* Oswald, 1990 and *B. lisae* Jepson, Ansorge & Jarzembowski, 2011, lack a pterostigmal crossvein in both fore- and hind wings (Oswald 1990: p. 156, figs 3, 4; Jepson et al. 2011: p. 393, text-figs 6A, B). Some genera can even show an additional, straight pterostigmal crossvein in a more basal position at least in the hind wing, i.e., *B. kolosnitsynae* Martynova, 1961 and *B. pulchra* (Martins-Neto and Nel, 1992) (Martynova 1961: p. 81, fig. 7; Martins-Neto and Nel 1992: p. 428, figs 2, 3). Regarding the other taxa currently classified within the Baissopteridae, the genera *Lugala* and *Cretoraphidia* lack a pterostigmal crossvein, at

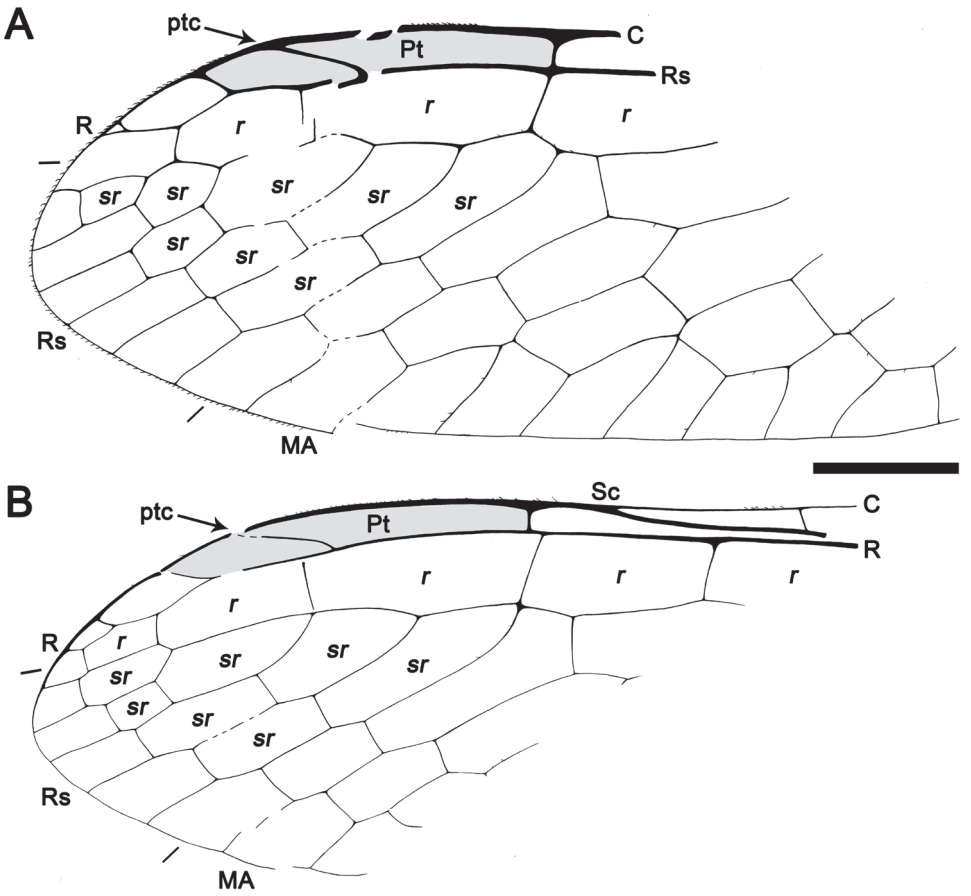

Figure 3. Drawings of *Baissoptera*? *cretaceoelectra* sp. n., holotype MCNA 12068.4. **A**, forewing **B** hind wing. Scale bar = 1 mm (both wings at the same scale).

least in the hind wing (Ponomarenko 1988: p. 75, fig. 4; 1993: p. 70, figs 7, 9, 10); whereas the genera *Cretoraphidiopsis* and *Austroraphidia*, although showing a pterostigmal crossvein situated beyond pterostigmal midlength, have it not as strongly oblique as in *B.*? *cretaceoelectra* sp. n., both showing irregular gradate series in both wings and a much lesser number of Rs branches in the forewing (three in *Austroraphidia*, four in *Cretoraphidiopsis*). *Cretinocellia cellulosa* Ponomarenko, 1988 has been recently transferred from the Baissopteridae to the Mesoraphidiidae by Bechly and Wolf-Schwenninger (2011) based on its lack of pterostigmal crossvein(s) and a Sc ending about midwing length. Although these two characters are also present in *Cretoraphidia certa* Ponomarenko, 1993 and *C. magna* Ponomarenko, 1993 (Ponomarenko 1993: p. 70, figs 7, 10), in both, the crossvenation is relatively higher than in *C. cellulosa* and should therefore remain in Baissopteridae for the moment. Consequently, Bechly and Wolf-Schwenninger (2011) also noted that the genus *Cretinocellia* might occupy a basalmost position within Mesoraphidiidae according to its relatively high crossvenation compared to the other mesoraphidiids. On the other

hand, we still consider *Arariperaphidia rochai* Martins-Neto and Vulcano, 1989 as incertae sedis rather than as a baissopterid (*contra* Bechly and Wolf-Schwenninger 2011), owing to its lack of preserved characters indicating a more conclusive assignment. The shape and location of the pterostigmal crossvein is quite diagnostic for *B.*? *cretaceoelectra*. Only *Baissoptera minima* Ponomarenko, 1993 shows such a strongly oblique pterostigmal crossvein within the family, even slightly sinusoid as in the new species, in a relatively elongate pterostigma (length ca. eight times basal pterostigmal width) (Ponomarenko 1993: p. 64, fig. 2). However, the pterostigmal crossvein is located before pterostigmal midlength and Rs is poorly branched in *B. minima*. *Baissoptera*? *cretaceoelectra* has Rs in the forewing with more branches currently described within the genus. The remaining *Baissoptera* species always show a lesser number of branches of Rs in the forewing, i.e., five (*B. brasiliensis*, *B. grandis* Ren in Ren et al., 1995, *B. liaoningensis* Ren, 1994, *B. lisae*, and *B. sibirica* Ponomarenko, 1993), four (*B. elongata* Ponomarenko, 1993, *B. euneura* Ren, 1997, *B. kolosnitsynae*, and *B. martinsoni* Martynova, 1961), or three Rs branches (*B. pulchra* and *B. minima*) (Martynova 1961; Oswald 1990; Martins-Neto and Nel 1992; Ponomarenko 1993; Ren 1994, 1997; Ren et al. 1995; Jepson et al. 2011). Although *B. cellulosa* Ponomarenko, 1993 (based on a forewing lacking the apex) could also possess six branches of Rs and does have a sinuate pterostigmal crossvein presumably beyond pterostigmal midlength (Ponomarenko 1993: p. 65, fig. 3), it differs from *B.*? *cretaceoelectra* in that the pterostigmal crossvein is just slightly oblique and the more abundant crossvenation. The only other described baissopterid with such an elevated number of branches of Rs is *Cretoraphidia certa*, but it lacks a pterostigmal crossvein as has been discussed, and in addition Sc ends in a more basal position. Furthermore, the pterostigmal length of the new species is elongate when compared to the other lengths shown by the other species within the genus *Baissoptera*. Only *B. grandis* has a longer pterostigma, its length about 11 times its basal pterostigmal width (Ren et al. 1995: p. 175, fig. 2). The shortest pterostigmata within the genus are found in *B. martinsoni* and *B. elongata*, their lengths ca. four and six times their basal pterostigmal widths, respectively (Martynova 1961: p. 80, fig. 6; Ponomarenko 1993: p. 67, fig. 5). Naturally, our placement of this species in *Baissoptera* is a conservative position based on the lack of complete material. More completely-preserved specimens, in which the wing base characters noted above could be assessed, may force a reconsideration of the generic assignment.

Family Mesoraphidiidae Martynov, 1925

Necroraphidia Pérez-de la Fuente, Peñalver, Delclòs & Engel, gen. n.

urn:lsid:zoobank.org:act:BF4F7D74-232F-4F2E-8754-E3940CD9D8B0
http://species-id.net/wiki/Necroraphidia

Type species. *Necroraphidia arcuata* sp. n.

Diagnosis. Small size; costal field very broad; pterostigma with a single, subdistal, strongly oblique, slightly sinuose to arcuate crossvein; pterostigma with a

diffuse base; forewing with Rs and MA each forked twice; forewing with second radial cell proximally broad.

Etymology. The new genus-group name is a combination of the Greek word *nekros*, meaning, "dead", and *Raphidia*, common generic stem for snakeflies. The name is feminine.

Comments. *Necroraphidia* gen. n. is most similar to *Ororaphidia* and *Styporaphidia* from the Late Jurassic of Inner Mongolia, China (Engel and Ren 2008). These three genera show the very diagnostic character of a diffuse base to the pterostigma, lacking a crossvein as the proximal boundary of this wing region (figs 4D–E). Also, they share the presence of, at least, one pterostigmal crossvein subdistally, three discoidal cells posterior to MP in the forewing (forming a triangle), and a larger size if compared with other minute mesoraphidiids. *Caloraphidia glossophylla* Ren, 1997 (combination restored by Bechly and Wolf-Schwenninger 2011) shares these three characters, but it lacks the diffuse pterostigmal base according to Ren (1997: p. 184, fig. 11). Hence, to consider this species as closely related (i.e., as an ororaphidiine in their system) as suggested by Bechly and Wolf-Schwenninger (2011) seems dubious. *Necroraphidia* can be separated from *Styporaphidia* by the presence of a single pterostigmal crossvein (two in *Styporaphidia*) and the three branches of both Rs and MA (two branches in *Styporaphidia*), while it can be distinguished most readily from *Ororaphidia* by the strongly oblique and arcuate shape of the pterostigmal crossvein (less oblique and straight in *Ororaphidia*), the proximally broader second radial cell (narrowly triangular proximad in *Ororaphidia*), the smaller second discoidal cell, and also by the smaller size (forewing length 11.4 in *Ororaphidia*) (Engel and Ren 2008).

Necroraphidia arcuata Pérez-de la Fuente, Peñalver, Delclòs & Engel, sp. n.

urn:lsid:zoobank.org:act:A0CA422D-FD60-4753-B8DE-7C5A4E75BDAE
http://species-id.net/wiki/Necroraphidia_arcuata
Figs 4, 5

Holotype. CES 391.1, from El Soplao amber; incomplete specimen, almost complete left fore- and hind wings (lacking their basalmost part), distal half of right hind wing and apex of right forewing, partial abdomen, and two leg fragments. Dense fungal hyphae infestate the abdomen and wings. The specimen is preserved together with the following syninclusions: two coleopterans, two hymenopterans (one of them, CES 391.2, belonging to the Megalyridae; Pérez-de la Fuente et al. 2012), one immature aphid, a cluster of trichomes, a few charcoalified plant fibers (Fig. 7A), a few timber debris, as well as other indeterminate organic remains.

Diagnosis. As for the genus (*vide supra*).

Description. Sex unknown. Legs patterned as follows (at least in the preserved fragments): femur with three dark areas, tibia with proximal area darkened and a dark area beyond midlength. Wing veins brown; veins with strong, very short setae, especially abundant on C; membrane hyaline. *Forewing*. Length of preserved frag-

Figure 4. *Necroraphidia arcuata* gen. et sp. n., holotype CES 391.1. **A** ventral habitus, note some charcoalified plant fibers nearby the specimen (arrow) **B** right forewing pterostigmal crossvein **C** right hind wing pterostigmal crossvein **D** right forewing pterostigmal diffuse base **E** right hind wing pterostigmal diffuse base. Scale bars: **A** = 2 mm; **B, C, D, E** = 0.5 mm.

ment 6.9 (estimated total wing length > 9), maximum width 2.7; costal field very broad (costal field about two times wider than pterostigmal base at widest preserved point; Sc terminating into C around two-thirds of estimated wing length; three c-sc

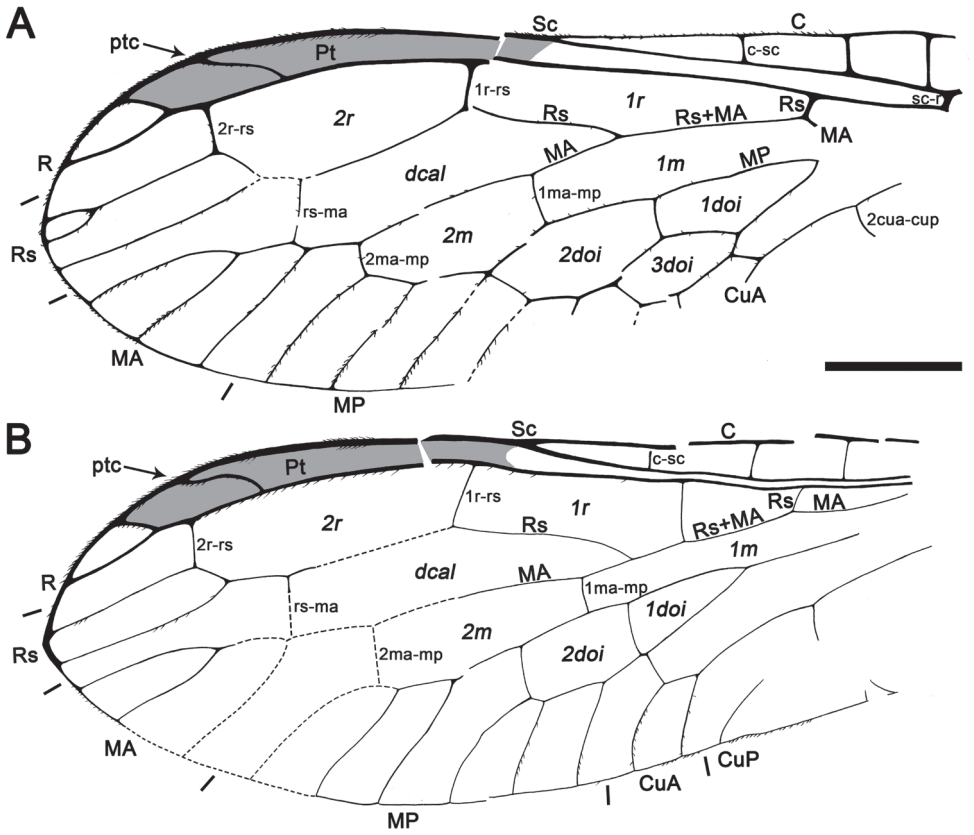

Figure 5. Drawings of *Necroraphidia arcuata* gen. et sp. n., holotype CES 391.1. **A** right forewing **B** right hind wing with reconstructed part taken from the left hind wing (dashed line). Only the distalmost c-sc crossvein has been tagged for both wings. Scale bar = 1 mm (both wings at the same scale).

crossveins preserved; single, proximal sc-r crossvein; pterostigma elongate (3.2 long, longer than either radial cell), widening distally (maximum width almost twice basal width), and faintly infumate, starting at termination of Sc; pterostigma with a single, subdistal, strongly oblique, slightly sinuose crossvein; pterostigma with a diffuse base (i.e., lacking a crossvein as proximal boundary of this wing region); Rs with three branches, distalmost fork very short; two large radial cells present; first radial cell about 1.3 times longer than second radial cell; second radial cell proximally broad; MA arising slightly distad midpoint of first radial cell, with three branches; three discoidal cells posterior to MP; 1cua-cup crossvein not preserved; anal veins not preserved; jugal lobe not visible. *Hind wing.* Length of preserved fragment 6.6 (estimated total wing length 8–9), maximum width 2.7; costal field distinctly narrower than in forewing; four c-sc crossveins preserved; pterostigma elongate (2.9 long, longer than either radial cell), widening distally (maximum width almost twice basal width), and faintly infumate, starting at termination of Sc; pterostigma with a single, subdistal, strongly oblique, arcuate crossvein; pterostigma with a diffuse base;

Rs with two branches; two radial cells present; MA with three branches; two discoidal cells posterior to MP, the first one trianguloid, not much smaller than second one; 1ma-mp crossvein not especially close to fork between Rs and MA; anal area not preserved. *Abdomen*. Length 3.8. Genitalia degraded, with dorsal part missing, and badly seen due to presence of dense fungal hyphae.

Etymology. The specific epithet is the Latin term *arcuatus*, meaning "bent", and refers to the arcuate form of the pterostigmal crossvein.

Genus *Styporaphidia* Engel & Ren, 2008

Styporaphidia? *hispanica* Pérez-de la Fuente, Peñalver, Delclòs & Engel, sp. n.

urn:lsid:zoobank.org:act:0AAD19B5-EF08-4B10-B704-DBF6D56A0D6F
Fig. 6

Holotype. MCNA 9343, from Peñacerrada I amber; hind wing fragment and abdominal apex, including the genitalia.

Diagnosis. The new species is similar to *Styporaphidia magia* Engel and Ren, 2008 from the Late Jurassic of Inner Mongolia, China, in the presence of two pterostigmal crossveins. *Styporaphidia*? *hispanica* sp. n. differs in that the distance between 1ptc and 2ptc is three times the distance between 2ptc and the end of the pterostigma (two times in *S. magia*), the forking of Rs at the apicalmost r-rs crossvein (rather than prior to it in *S. magia*), and R meeting the apicalmost r-rs crossvein beyond the pterostigma (within in *S. magia*).

Description. Male. *Hind wing.* Length as preserved 3.5, maximum width as preserved 2.5; wing apex relatively rounded; C especially thick when compared to other veins; pterostigma almost with constant width along its entire length, infumate; pterostigma with two crossveins, distalmost crossvein oblique and slightly arcuate, proximal crossvein apparently straight, distance between 1ptc and 2ptc three times distance between 2ptc and end of pterostigma; Rs with two branches, forking at r-rs crossvein; R meeting apicalmost r-rs crossvein beyond pterostigma; rs-ma crossvein meeting MA after its distalmost fork; MA with two branches. *Abdomen.* Gonocoxites 9 with a few long setae; gonostyli 9 segment rather short, rounded (not acute), slightly upcurved; tergite 10 (+11?) with distal setae; paired, contiguous, acute genital structures located dorsad to gonostyli 9, interpreted as distalmost part of parameres (Fig. 6A).

Etymology. The specific epithet refers to the occurrence of this species in ancient Spain (*Hispania* in Latin).

Comments. Although the base of the pterostigma is not preserved and it is accordingly impossible to ascertain if it was diffuse (i.e., lacking a crossvein), this species is tentatively placed in the genus *Styporaphidia* owing to the presence of two pterostigmal crossveins. The presence of two pterostigmal crossveins is a rare feature among the Raphidioptera and otherwise known in a few other raphidiopterans, i.e, namely the baissopterids *B. kolosnitsynae* and *B. pulchra* (Martynova 1961: p. 81, fig. 7; Martins-

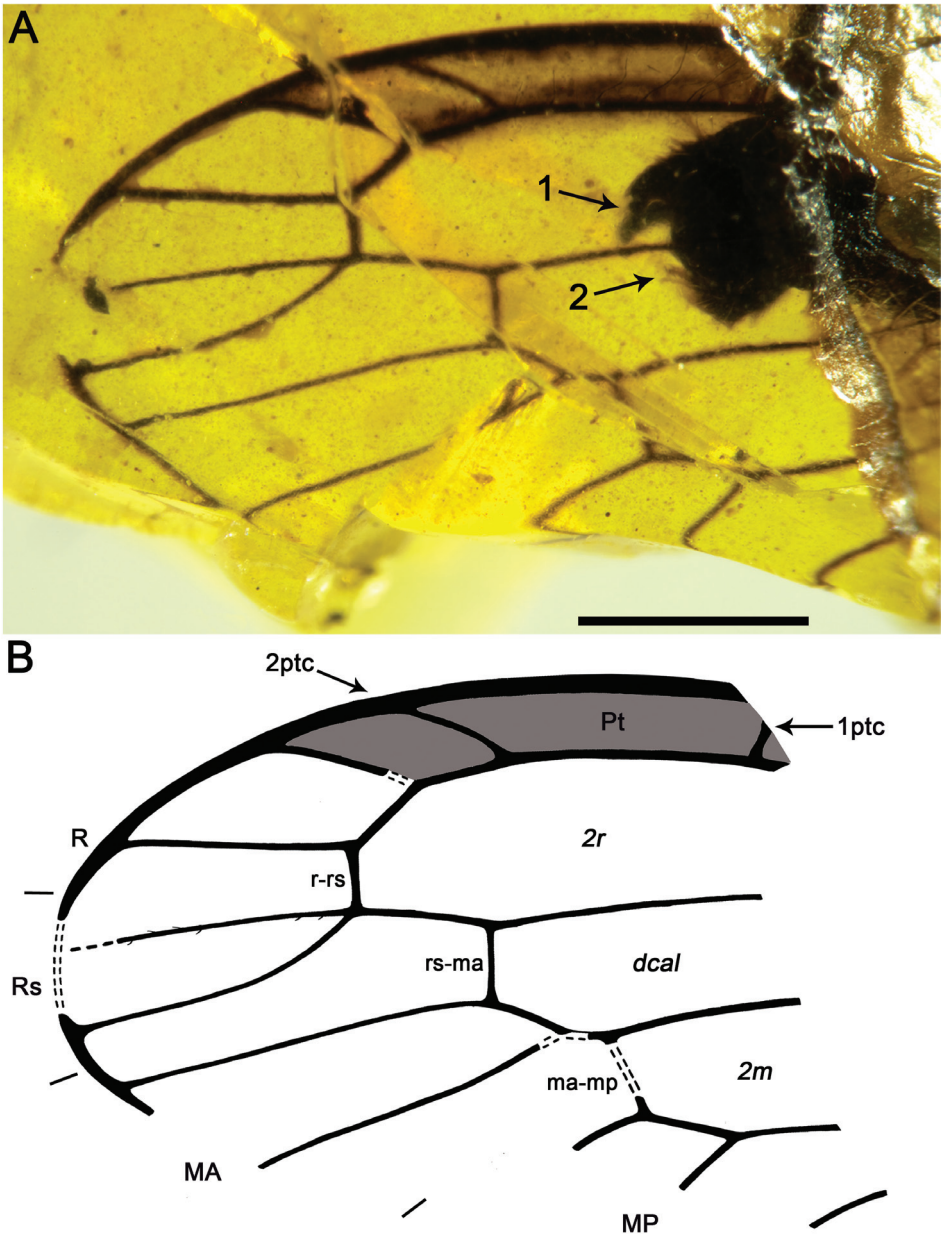

Figure 6. *Styporaphidia*? *hispanica* sp. n., holotype MCNA 9343. **A** hind wing apical fragment and genitalia; arrow 1 points to gonostyli 9, whereas arrow 2 points to the paired genital sclerites interpreted as the distalmost part of the parameres **B** drawing of preserved hind wing apical fragment. Scale bar = 1 mm.

Neto and Nel 1992: p. 428, figs 2, 3), but the present fossil is clearly not a baissopterid. The fragment is considered as corresponding to a hind wing due to the more distal disposition of both crossveins as occurs in *S. magia* (the distance between them being

greater than the distance between 2ptc and the end of the pterostigma), and by the relative position of the abdomen. The veins C and R appear to be especially thickened close to the wing apex as occurs also in *S. magia* (Engel and Ren 2008: fig. 2), though this effect could be enhanced by the darkening of the margins of the pterostigma. Although the species is represented by a wing fragment and the genitalia, it is distinctive enough that it should be easy to associate with more complete material that may become available in the future.

Amarantoraphidia Pérez-de la Fuente, Peñalver, Delclòs & Engel, gen. n.

urn:lsid:zoobank.org:act:EA2F19D0-E3C8-43A7-BA92-BFC73C2FA208
http://species-id.net/wiki/Amarantoraphidia

Type species. *Amarantoraphidia ventolina* sp. n.

Diagnosis. Minute size. Head ovoid, with the portion posterior to the compound eyes longer than the eye diameter and tapering caudad; three large ocelli present, situated between anterior half of compound eyes; antennae with a low number of flagellomeres (i.e., ≤ 26). Pronotum slightly longer than head, with a constant height along its entire length. Mesotibiae especially swollen; process at midlength of the metatibiae absent. Forewing with costal field moderately broad; pterostigma elongate, without crossveins; Sc terminating into C slightly distad wing midlength; six c-sc crossveins present; two discoidal cells posterior to MP; apicalmost branch of CuA simple; 1cua-cup crossvein located at the M-CuA separation.

Etymology. The new genus-group name is a combination of the Greek term *amarantos*, meaning "that never fades, ageless", and *Raphidia*, common generic stem for snakeflies. The name is feminine.

Comments. *Amarantoraphidia* gen. n. is first compared with the other described minute mesoraphidiid genera, which have a forewing length around 6 or less. They include amber inclusions but also some compression fossils. Apart from the minute size, in all of these taxa the pterostigma is very elongate, without crossveins, and basally closed by a crossvein. Regarding those as amber inclusions, *Amarantoraphidia* is readily distinct from the other two currently described Spanish mesoraphidiid genera, *Cantabroraphidia* and *Alavaraphidia* gen. n., as well as *Lebanoraphidia*, by its ovoid head shape (subquadrate in *Cantabroraphidia*, and rhomboidal in the other two genera) and by its lesser number of antennal flagellomeres (26 flagellomeres in *Cantabroraphidia*, 38 flagellomeres or more in *Lebanoraphidia*, and 44 in *Alavaraphidia*). The two genera *Nanoraphidia* (type species *N. electroburmica* Engel, 2002, Burmese amber, latest Albian in age) and *Grimaldiraphidia* (type species *G. luzzi* (Grimaldi, 2000), New Jersey amber, Turonian in age) share with *Amarantoraphidia* the ovoid head shape. However, in both of these genera the ocelli are placed between the posterior half of the compound eyes, not between the anterior part as in *Amarantoraphidia*. Additionally, whereas *Amarantoraphidia* has two discoidal cells posterior to MP in the forewing, *Grimaldiraphidia* has three and *Nanoraphidia* just a single

cell. Also, in *Nanoraphidia* the M-CuA separation is located near midpoint of the first and second cua-cup crossveins (Engel 2002; Jepson et al. 2011), not at the 1cua-cup crossvein as in *Amarantoraphidia*.

In addition to the aforementioned taxa, five mesoraphidiids with minute size have been hitherto described from compression fossils: *Grimaldiraphidia parvula* (Martynov, 1925), from Karatau (South Kazakhstan), Late Jurassic in age; *G. mitchelli* (Jepson, Coram and Jarzembowski, 2009), *G. purbeckensis* Jepson, Coram and Jarzembowski, 2009, and *Mesoraphidia websteri* Jepson, Coram and Jarzembowski, 2009, the three species from the Purbeck Limestone Group, Dorset (UK), Berriasian in age; and *Nanoraphidia lithographica* Jepson, Ansorge and Jarzembowski, 2011 (tentatively assigned to this genus), from El Montsec (Spain), Early Barremian in age. *Grimaldiraphidia parvula* (described from a complete specimen but its wings unresolved dorsoproximally) has more proximal positions of the fork of Rs and the 2r-rs and rs-ma crossveins than *Amarantoraphidia* (Martynov 1925: p. 242, figs 7–9). *Grimaldiraphidia mitchelli* (described from a wing, most likely a forewing, with not preserved base and pterostigma), although possessing two discoidal cells posterior to MP as in the forewing of *Amarantoraphidia*, has a venation somewhat different, with the second radial cell relatively wide compared to its length, and more proximal positions of the fork of Rs and the 2r-rs and rs-ma crossveins (Jepson et al. 2009). *Grimaldiraphidia purbeckensis* possesses three discoidal cells posterior to MP in the forewing, the M-CuA separation is located near midpoint of the first and second cua-cup crossveins, and has more proximal positions of the fork of Rs and the 2r-rs and rs-ma crossveins (ibid.). *Mesoraphidia websteri* (based on a hind wing) has the Sc ending beyond the first radial cell, relatively shorter second radial and discal cells, and a single discoidal cell (two discoidal cells posterior to MP in *Amarantoraphidia*) (ibid.). Lastly, *N. lithographica* shows only one discoidal cell posterior to MP in the forewing as in the type species for the genus, *N. electroburmica* (Jepson et al. 2011).

Amarantoraphidia ventolina Pérez-de la Fuente, Peñalver, Delclòs & Engel, sp. n.

urn:lsid:zoobank.org:act:79F0A7A3-789D-4B3F-8E34-A021073A86AD
http://species-id.net/wiki/Amarantoraphidia_ventolina
Figs 7–9

Holotype. CES 364.1, from El Soplao amber; almost complete female, just lacking the distalmost portion of both forewings beyond the end of the pterostigma and the distal third of the right hind wing. The first left leg is disarticulated. The specimen is preserved together with the following syninclusions: one evaniid (a new *Cretevania* species; CES 364.2, Pérez-de la Fuente et al. 2012, in prep.) and three other indeterminate hymenopterans, four dipterans (one chimeromyiid among them), one thysanopteran, a few charcoalified plant fibers, and a few timber debris, as well as other indeterminate organic remains.

Diagnosis. As for the genus (*vide supra*).

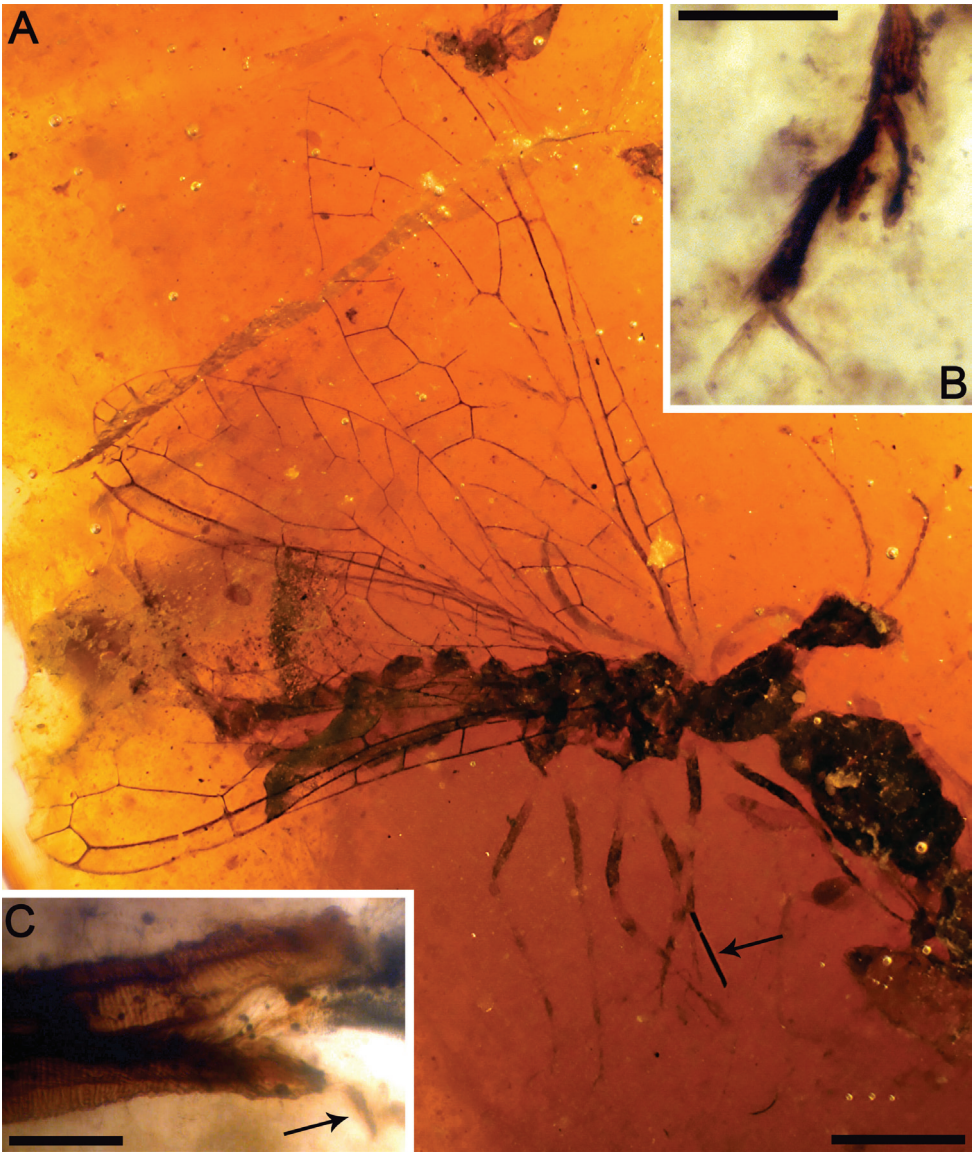

Figure 7. *Amarantoraphidia ventolina* gen. et sp. n., holotype CES 364.1. **A** lateral habitus, note a charcoalified plant fiber nearby the specimen (arrow) **B** left metatarsi showing bilobed third tarsomere **C** distal portion of ovipositor, note its dense annulation; arrow points to a gonostylus. Scale bars: **A** = 1 mm; **B, C** = 0.1 mm.

Description. Female. Integument dark brown; legs patterned as follows: femora darkened from just before their midlength to their end; three dark areas on tibiae, proximally, medially and distally; tarsomere 1 not darkened, distal tarsomeres darkened. *Head.* Ovoid, about 0.7–0.8 long, with portion posterior to compound eyes longer than eye diameter and tapering caudad; three large ocelli present, situated between an-

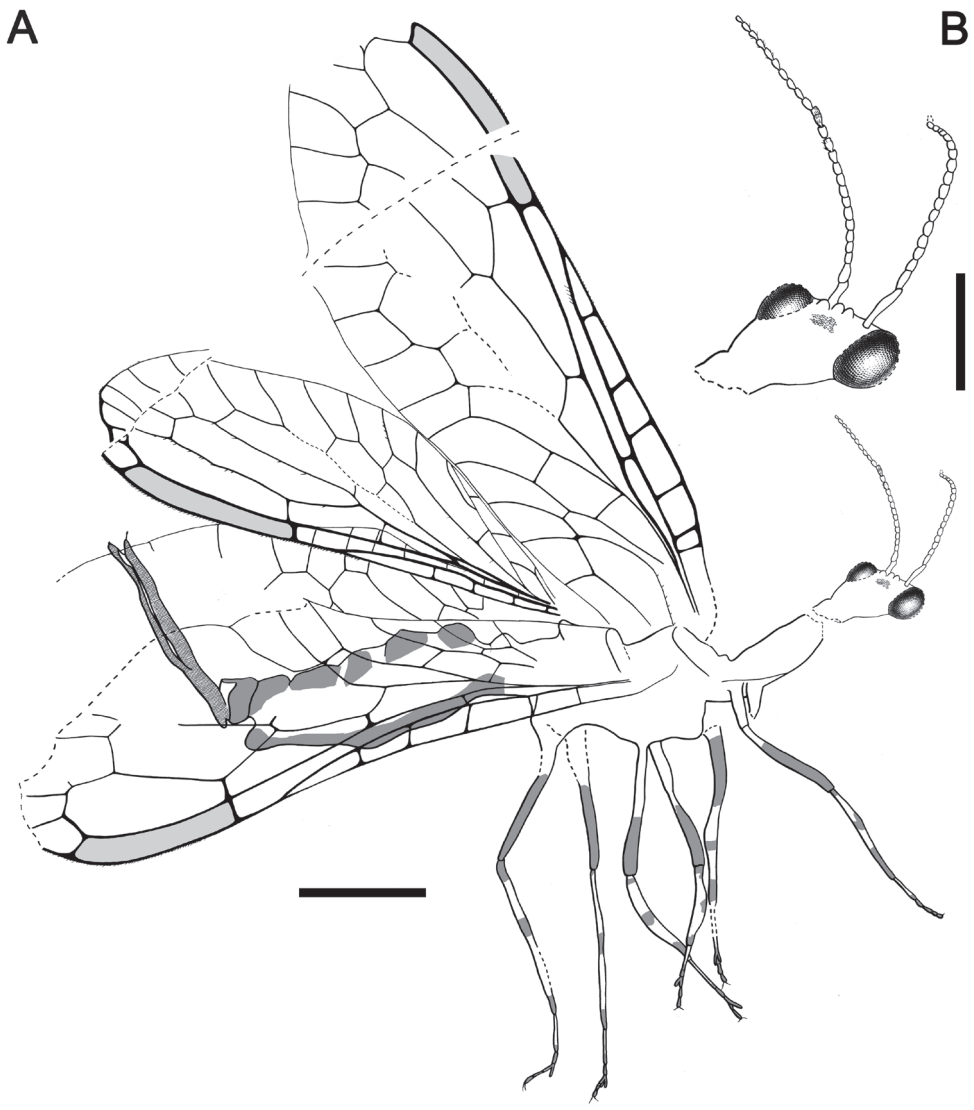

Figure 8. Drawings of *Amarantoraphidia ventolina* gen. et sp. n., holotype CES 364.1. **A** lateral habitus **B** head, magnified. Scale bars: **A** = 1 mm; **B** = 0.5 mm.

terior half of compound eyes; mandibles with teeth not visible; palps short; compound eyes large and exopthalmic, separated by distance slightly greater than compound eye length; antennae inserted around anterior tangent of compound eyes (exact insertion not visible); scape and pedicel gracile, both measuring about length of four flagellomeres and being subequal in thickness to them; 24 flagellomeres present, slightly longer than wide, with sparse, minute setae; coronal ecdysial cleavage line not evident; posterior border of head with a distinct collar-like lip. *Thorax.* Prothorax about 1.1 long, meso- plus metathorax 1.4 long; pronotum slightly longer than head, with a constant

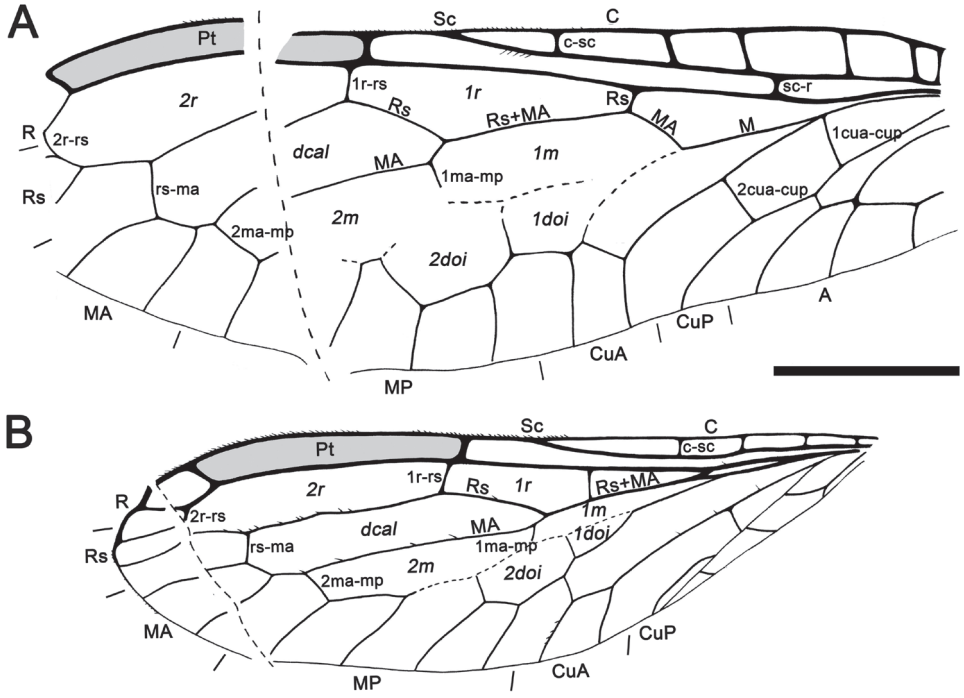

Figure 9. Drawings of *Amarantoraphidia ventolina* gen. et sp. n., holotype CES 364.1. **A** left forewing **B** left hind wing, depicted with its preservational folding, i.e., the basal part of MA is superimposed by the basal part of MP and the anal field is folded upwards. Only the distalmost c-sc crossvein has been tagged for both wings. Scale bar = 1 mm (both wings at the same scale).

height along its entire length (i.e., without a distinct change of slope in lateral view); a few spines visible on prothorax, dorsoanterior mesothorax apparently with a few small spines; all tibiae with apical spines; mesotibiae especially swollen; metatibiae significantly more elongate and thinner than the other tibiae; process at midlength of metatibiae absent; five tarsomeres, third with bilobed extensions lacking digitiform processes (Fig. 7B); pretarsal claws simple, with a basal enlargement; arolium large. Wing veins brown, meeting wing margins without bifurcating; veins with strong, very short setae, especially abundant on C; membrane hyaline. *Forewing.* Length about 5.6 (tip not preserved), maximum width 1.9; costal field moderately broad (at widest point costal field about 1.4 wider than pterostigma); six c-sc crossveins present, two basalmost c-sc crossveins particularly close to each other; Sc terminating into C slightly distad wing midlength; single, proximal sc-r crossvein; pterostigma elongate (1.5 long), slightly longer than either radial cell; pterostigma with constant width along its entire length, faintly infumate, starting 0.4 (about three times pterostigmal width) beyond termination of Sc; pterostigma without crossveins, basally closed by a crossvein; Rs with two branches; two large radial cells present; first radial cell nearly as long as second radial cell, with MA arising slightly distad its midpoint; MA with two branches; two dis-

coidal cells posterior to MP; apicalmost branch of CuA unforked; 1cua-cup crossvein located at M-CuA separation; 2A arcuate; jugal lobe not visible. *Hind wing.* Length about 4.1, maximum width 1.3; costal field distinctly narrower than in forewing; four c-sc crossveins present; sc-r crossvein absent; pterostigma elongate (1.5 long), slightly longer than second radial cell; pterostigma with about a constant width along its entire length, faintly infumate, starting 0.3 (slightly more than two times pterostigmal width) beyond termination of Sc; pterostigma without crossveins, basally closed by a crossvein; Rs with two branches; two radials cells present; MA with two branches; two discoidal cells posterior to MP, first one smaller and trianguloid; 1ma-mp crossvein close to fork between Rs and MA; anal area folded. *Abdomen.* Length 2.4; ovipositor robust, 1.7 long as preserved, 0.1 thick (about 15 times as long as wide); ovipositor showing dense annulations (Fig. 7C); ovipositor with faint, stiff, short sensory setae along its entire length; ovipositor gonostyli most likely club-shaped.

Etymology. In the Cantabrian mythology, the "ventolines" are tenacious and always cheerful fairy-like air beings that dwell in the depths of the sky and, when summoned, help defenseless fishermen by placidly steering their boats to the shore while embracing them with their warm green wings. The term has been singularized and feminized for combination.

Comments. In extant snakeflies, the dense annulations of the ovipositor (cf. Fig. 7C) provide the flexibility necessary for introduction into irregular cavities, similar to a flexible metallic hose (Mickoleit 1973). It has been noted how mesoraphidiids would have had a shorter and thicker ovipositor than Recent Raphidioptera (Bechly and Wolf-Schwenninger 2011). The shape of the ovipositor in this specimen and also in *Alavaraphidia* gen. n. supports such a conclusion.

Alavaraphidia Pérez-de la Fuente, Peñalver, Delclòs & Engel, gen. n.

urn:lsid:zoobank.org:act:070A3E8E-1F78-4663-A909-1872E5EEA80E
http://species-id.net/wiki/Alavaraphidia

Type species. *Alavaraphidia imperterrita* sp. n.

Diagnosis. Minute size. Head rhomboidal, with clypeus especially elongate and the portion posterior to the compound eyes shorter than the eye diameter and strongly tapering caudad; three large ocelli present, situated near the posterior tangent of compound eyes; antennae extremely elongate, with a high number of flagellomeres (i.e., ≥ 38). Pronotum shorter than head, with a constant height along its entire length. All tibiae especially swollen medio-apically; process at midlength of the metatibia indistinct. Bilobed extensions of third tarsomeres with distal digitiform processes.

Etymology. The new genus-group name is a combination of Álava, from Álava amber (the name of the group for Peñacerrada I and Peñacerrada II amber localities), and *Raphidia*, common generic stem for snakeflies. The name is feminine.

Comments. Although most of the wings are not preserved, the other features of *Alavaraphidia* gen. n. are distinctive enough to justify the creation of a distinct taxon.

The minute size of *Alavaraphidia* mainly limits its comparison to other minute taxa mainly described from amber inclusions (refer to comments for *Amarantoraphidia* gen. n.). Although a few other taxa based on wings from compressions are minute in size it is not possible to compare them with the new genus and species due to the absence of most of its wings. The genus *Lebanoraphidia* shares with *Alavaraphidia* the rhomboidal shape of the head with the compound eye length greater than that of the head posterior to the eyes (Bechly and Wolf-Schwenninger 2011); the head shape is ovoid in the genera *Grimaldiraphidia*, *Nanoraphidia*, and *Amarantoraphidia*, and subquadrangular in the genus *Cantabroraphidia*. Moreover, the genus *Lebanoraphidia* differs from *Alavaraphidia* in the lesser number of flagellomeres (note how the number of flagellomeres depicted for *L. nana* Bechly and Wolf-Schwenninger, 2011, type and only species of the genus, seems to not match the description and photographs), the shorter clypeus, the shorter portion posterior to the compound eyes, the longer relative length of the pronotum, and the assumed absence of distal digitiform processes on the third tarsomere's bilobed extensions. The high number of flagellomeres of *Alavaraphidia* (44) is most similar to that of *Lebanoraphidia*, itself with around 38 flagellomeres (Bechly and Wolf-Schwenninger 2011). Otherwise, 20 flagellomeres are present in the genus *Nanoraphidia* (Engel 2002), 23 in *Grimaldiraphidia* (Grimaldi 2000), 24 in *Amarantoraphidia*, and 26 in *Cantabroraphidia* (Pérez-de la Fuente et al. 2010). The distal digitiform processes from the third tarsomere's bilobed extensions (fig. 10C) have not been reported from any other taxon and thus it is considered a unique character. Regarding the leg patterning, the medial dark patch found on the tibia in *Cantabroraphidia* (ibid.) and *Amarantoraphidia* is absent in *Alavaraphidia*. However, this character is not considered relevant at the generic level and hence has been discarded from the present diagnosis.

***Alavaraphidia imperterrita* Pérez-de la Fuente, Peñalver, Delclòs & Engel, sp. n.**
urn:lsid:zoobank.org:act:E1406721-46BE-4F26-869E-EC6C5AE6CD01
http://species-id.net/wiki/Alavaraphidia_imperterrita
Figs 10, 11

Holotype. MCNA 13608, from Peñacerrada I amber; partial specimen showing head and ventral parts of thorax and abdomen, including the ovipositor. Only the basalmost part of the wings is preserved.

Diagnosis. As for the genus (*vide supra*).

Description. Female. Body length excluding ovipositor 5.7. Integument dark brown; legs patterned as follows: femora darkened from just before their midlength to their end; two dark regions on tibiae, proximally and distally (medial dark region absent); tarsomere 1 not darkened, distal tarsomeres darkened. *Head.* Rhomboidal, about 1.2 long, with portion posterior to compound eyes shorter than eye diameter (about 0.7 times) and strongly tapering caudad; three large ocelli present, situated near posterior tangent of compound eyes; mandible with teeth not visible; palps short; clypeus especially elongate; compound eyes separated by about compound eye length;

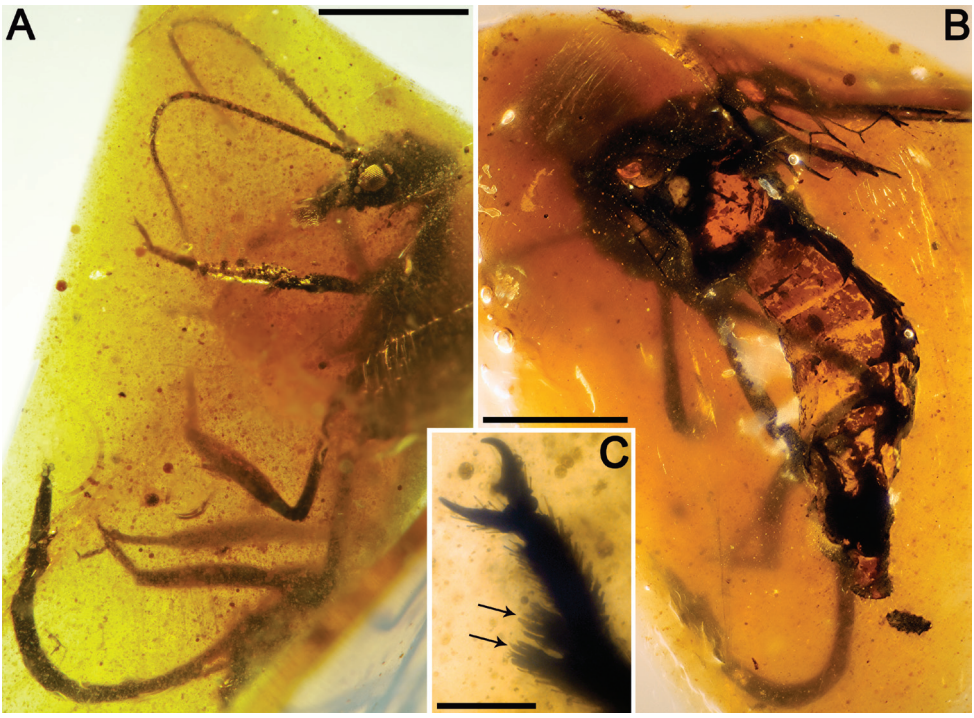

Figure 10. *Alavaraphidia imperterrita* gen. et sp. n., holotype MCNA 13608. **A** lateral habitus **B** dorsal habitus **C** left distal foretarsus, showing bilobed third tarsomere with digitiform processes (arrows). Scale bars: **A, B** = 1 mm; **C** = 0.1 mm.

three large ocelli present, situated near posterior tangent of compound eyes; antennae inserted posterior to clypealfrons sulcus, basad anterior tangent of compound eyes; antennae extremely elongate, with 44 flagellomeres; flagellomeres elongate, about 1.5 times longer than wide; scape and pedicel thicker than flagellomeres, scape measuring about two flagellomeres, pedicel measuring slightly more than a flagellomere; coronal ecdysial cleavage line not evident; posterior border of head not visible. *Thorax.* Prothorax about 0.8 long; meso- and metathorax about 1.1 long; pronotum shorter than head, with a constant height along its length (i.e., without a distinct change of slope in lateral view); thoracic dorsal spines not visible, if present; all tibiae especially swollen medio-apically, with apical spines, spines also visible on metatarsomeres; process at midlength of metatibia indistinct; five tarsomeres, third with bilobed extensions having six to eight distal digitiform processes (Fig. 10C), different in shape than regular leg setae (not tapering apically); pretarsal claws simple, with a basal enlargement; arolium large. Preserved wing veins brown, with strong, very short setae; preserved membrane hyaline. *Forewing.* Costal field not especially broad. Three c-sc crossveins preserved. *Hind wing.* Costal field distinctly narrower than in forewing. Three c-sc crossveins preserved. *Abdomen.* Length 2.7; ovipositor robust but rather elongate, about 2.7 long as preserved, 0.2 thick (about 15 times as long as wide); ovipositor with dense an-

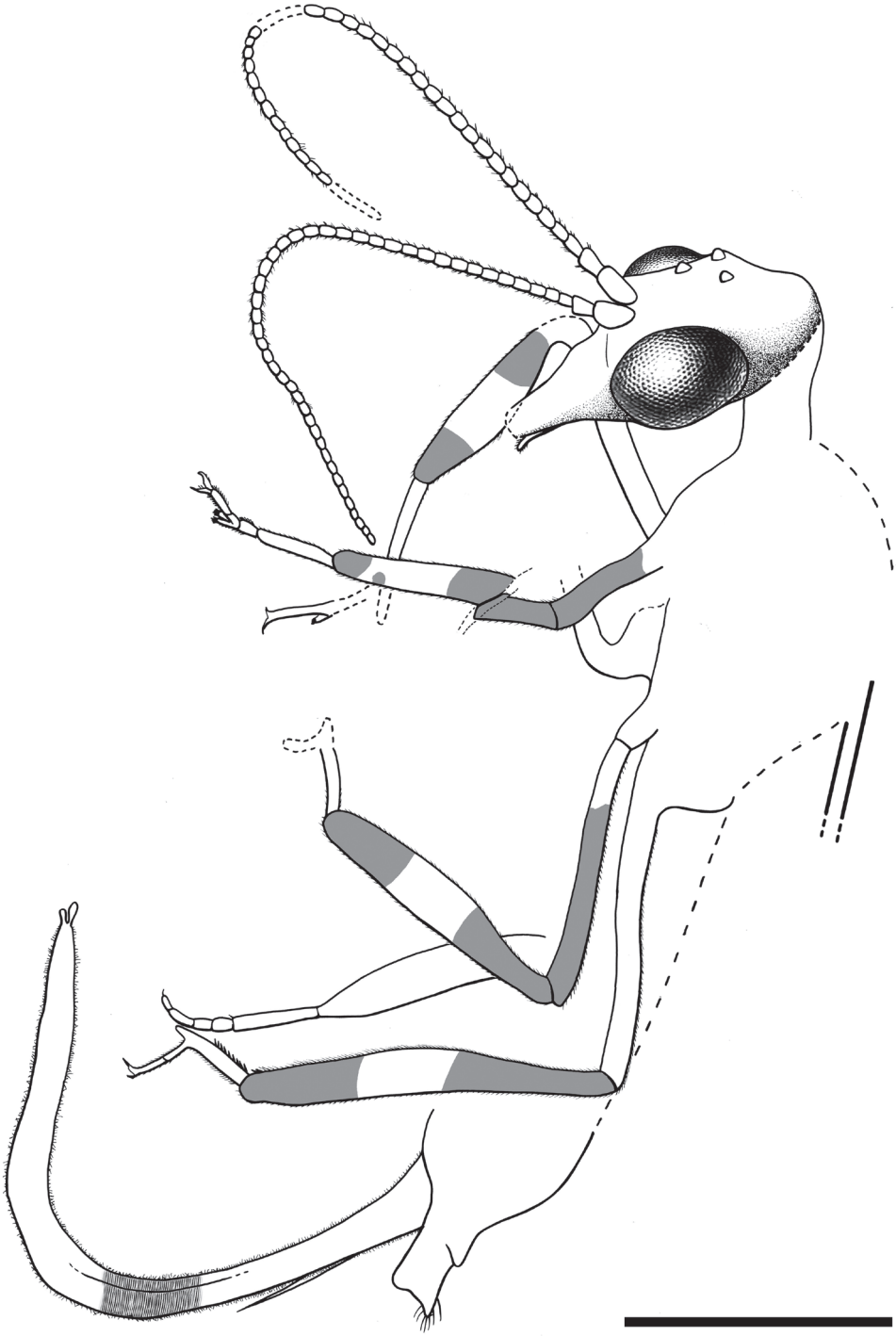

Figure 11. Drawing of *Alavaraphidia imperterrita* gen. et sp. n., holotype MCNA 13608. Lateral habitus. The annulations of the ovipositor have been depicted partially. Scale bar = 1 mm.

nulations; ovipositor with conspicuous faint, stiff, small sensory setae along its entire length; ovipositor gonostyli club-shaped; tergite 10 (+11?) with a distalmost stripe of stiff trichobothria (some probably from tergite 9).

Etymology. The specific epithet is the Latin term *imperterritus*, meaning "fearless", and symbolizes the unalterable condition of an organism entrapped in amber.

Genus *Cantabroraphidia* Pérez-de la Fuente, Nel, Peñalver & Delclòs, 2010

http://species-id.net/wiki/Cantabroraphidia
Fig. 12

Cantabroraphidia Pérez-de la Fuente, Nel, Peñalver, and Delclòs, 2010: 109. Type species: *Cantabroraphidia marcanoi* Pérez-de la Fuente, Nel, Peñalver, and Delclòs, 2010, by original designation.

Comments. According to the original diagnosis, this monospecific genus was characterized by the following combination of characters: minute size (forewing length 5.5). Head more or less quadrangular; with portion posterior to the compound eyes slightly shorter than the eye diameter and not tapering caudad; three large ocelli present, situated between anterior half of the compound eyes; posterior border of head with a distinct collar-like lip. Pronotum subequal in length to head length, with anterior half narrowed dorsoventrally relative to posterior half (i.e., with slight downward curve in lateral view). Process present at midlength of the metatibiae in a posterior position. Forewing with costal field relatively broad (at widest point costal field as broad as pterostigma); pterostigma elongate, without crossveins; Sc terminating into C in distal two-thirds of wing length; four c-sc crossveins; two discoidal cells posterior to MP; 1cua-cup crossvein strongly basad M-CuA separation; posterior branch of MP forked. Refer to Pérez-de la Fuente et al. (2010) for a complete description of the type and only known species from El Soplao amber, based on an adult of unknown sex.

Genus and species indet. 1

Figs 13A, 14A

Material. MCNA 9218, from Peñacerrada I amber; wing apex plus two minute wing fragments lacking formal descriptive significance. The sample consists of part and counterpart after the amber piece broke following the plane of the inclusion.

Descriptive notes. Sex unknown. *Hind wing(?).* Length of preserved fragment 2.4, maximum width of preserved fragment 2.4; wing apex rounded; pterostigma slightly increasing in width distally, infumate; pterostigma with an almost straight subdistal crossvein; all apical branches relatively short; Rs with three branches, distalmost fork

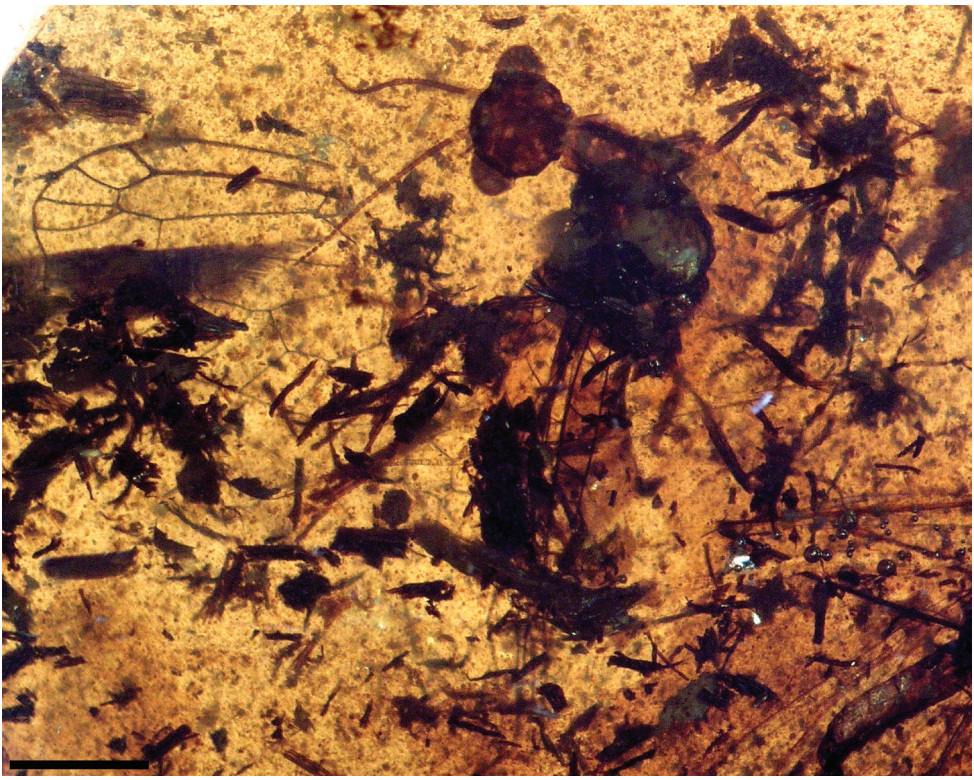

Figure 12. *Cantabroraphidia marcanoi* Pérez-de la Fuente et al., 2010. Laterodorsal habitus. Sex unknown. Note the abundant presence of timber debris in the amber piece, surrounding the specimen. Scale bar = 1 mm.

very short; apicalmost r-rs crossvein (2r-rs?) meeting R distal to the pterostigma; rs-ma crossvein situated at distalmost fork of MA; MA with two branches.

Comments. The present material is distinct from other Spanish amber snakeflies but does not preserve enough detail to permit formal designation as a taxonomic entity. The presence of a pterostigmal crossvein immediately discounts *Cantabroraphidia* and *Amarantoraphidia* gen. n. MCNA 9218 highly resembles the hind wing of *Styporaphidia* in the shape and location of the distalmost pterostigmal crossvein. In fact, its venation is very similar to *S.*? *hispanica* sp. n., though in the present material Rs is forked very close to the wing margin and the shape of its distalmost radial cell (most likely the second one) is somewhat different. Furthermore, the less pointed wing apex, shorter apical branches, and apical shapes of the radial, discal, and presumed second medial cells immediately distinguish MCNA 9218 from *Necroraphidia* gen. n. and genus and species indet. 2 (*vide infra*), and the almost straight pterostigmal crossvein and positions of the apicalmost r-rs (2r-rs?), rs-ma, and apicalmost ma-mp (2ma-mp?) crossveins further differentiate MCNA 9218 from *Necroraphidia*.

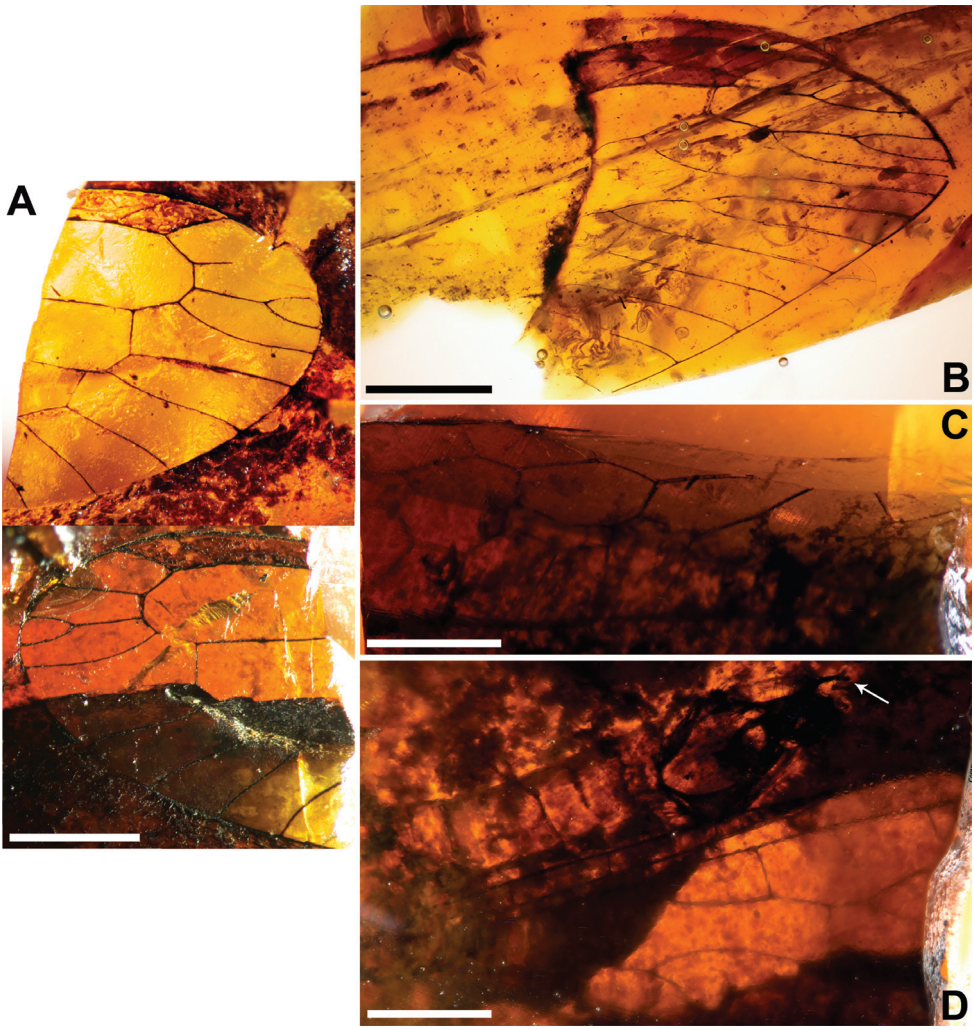

Figure 13. Fragmentary wing remains, genus and species indeterminate: CES 9218 part and counterpart (**A**), CES 376 (**B**), and MCNA 9316 (**C–D**). **A** distal part of a hind wing(?), part (above) and counterpart (below) **B** preserved distal wing fragments **C** preserved part of forewing **D** preserved part of hind wing and distal part of abdomen. Arrow points to the tip of right gonostylus 9. Scale bars = 1 mm.

Genus and species indet. 2
Figs 13B, 14B

Material. CES 376, from El Soplao amber; forewing apex and the area surrounding pterostigma from an additional wing. Some additional dorsoproximal parts of the wing are also present but with a very poor preservation, so just a few more characters can be elucidated. An indeterminate hymenopteran is present as a syninclusion.

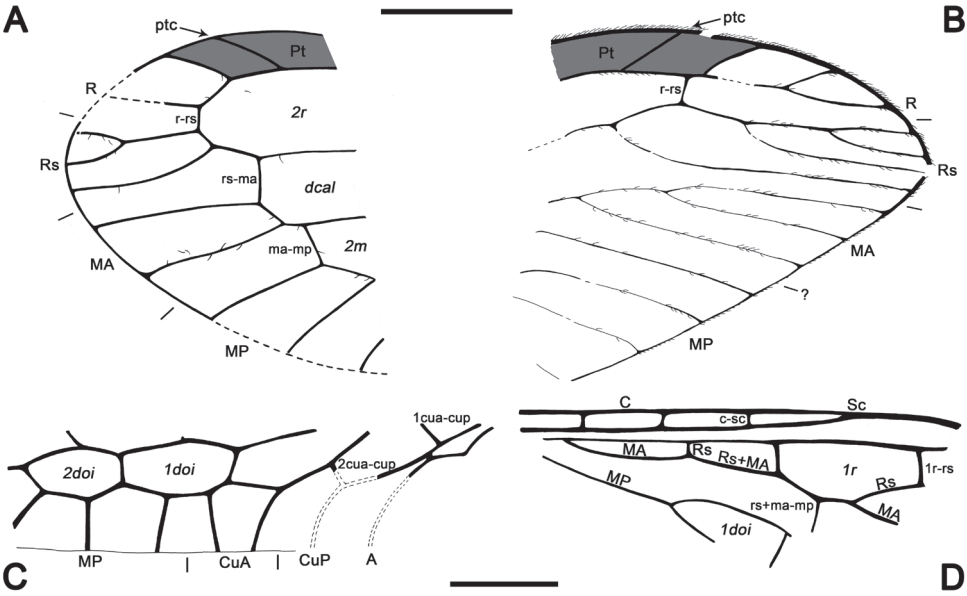

Figure 14. Drawings of fragmentary wing remains, genus and species indeterminate: CES 9218 counterpart (A), CES 376 (B), and MCNA 9316 (C–D). **A** distal part of hind wing(?) **B** best preserved distal wing fragment **C** preserved part of forewing **D** preserved part of hind wing; only the distalmost c-sc crossvein has been tagged; basalmost preserved c-sc crossvein not depicted. Scale bars = 1 mm (**A** and **B**; **C** and **D** at the same scale).

Descriptive notes. Length as preserved ca. 5.0 (wing well preserved only in 3.4 of that length), maximum width as preserved 2.7; wing apex pointed, positioned within Rs series; wing veins brown, meeting wing margins without bifurcating; veins with strong, short setae, especially abundant on C; Sc ending and proximal r-rs crossvein (1r-rs?; very faintly preserved) situated at about same wing length, pterostigma slightly widening distally, infumate; pterostigma with a very faint subdistal, rather straight (not conspicuously arcuate), strongly oblique crossvein; uncertain if pterostigmal division present; apical branches of Rs, MA and MP subparallel; two apical branches of R distal to pterostigma; Rs with four branches, posteriormost originating before distalmost r-rs crossvein (2r-rs?), separated from it by much more than its length; rs-ma and distalmost ma-mp crossveins lacking in preserved wing fragment, so most likely with a proximal position; MA most likely with three branches.

Comments. Despite the fact that CES 376 is distinct from the other taxa in Spanish amber, it is not named as its preserved parts are not enough to resolve its affinities. The wing fragments show a high resemblance with some mesoraphidiids such as *Mesoraphidia obliquivenatica* (Ren, 1994) and *Caloraphidia glossophylla*, both from the Cretaceous compression deposit of Liaoning (China), as long as all of them share the presence of a strongly oblique, rather straight pterostigmal crossvein in a

rather distal position and a distal portion of the wing with long apical branches and without crossveins other than the 2r-rs crossvein (Ren 1994: p. 134, fig. 4; 1997: p. 184, fig. 11). *Caloraphidia glossophylla* possesses subparallel apical branches of Rs, MA and MP, the Sc ending and the 1r-rs crossvein situated at about the same wing length, the 2r-rs crossvein closer to the end of the pterostigma than to the pterostigmal crossvein, and a pointed apex positioned within the Rs series, but in this species Rs has only three branches. By contrast, although *M. obliquivenatica* has Rs with four branches as in CES 376, the apical branches of Rs, MA and MP are not subparallel, the Sc ends in a more basal position than the 1r-rs crossvein, the 2r-rs crossvein is closer to the pterostigmal crossvein than to the end of the pterostigma, and the apex is more rounded and positioned between R and Rs. CES 376 is also quite similar to the wing apex of the compression fossil *Iberoraphidia dividua* Jepson, Ansorge and Jarzembowski, 2011, from El Montsec (Spain), Early Barremian in age, with its relatively simple venation, a Sc ending and a 1r-rs crossvein situated at about the same wing length, the 2r-rs, rs-ma and 2ma-mp crossveins not apically placed, the four branches of Rs, with the posteriormost branch of Rs originating before the 2r-rs crossvein, and the relatively simple apical fork of MA and MP (Jepson et al. 2011). CES 376 differs, however, in the presence of a pterostigmal crossvein (although in *I. dividua* the distal portion of the divided pterostigma could be basally closed by a crossvein), only two apical branches to R distal to the pterostigma (not three as in *I. dividua*), the posteriormost branch of Rs more proximally placed (separated from the distalmost r-rs by much more than its length, versus much shorter in *I. dividua*), and the more pointed wing apex which is positioned within the Rs series (rather than between R and Rs in *I. dividua*).

Genus and species indet. 3
Figs 13C–D, 14C–D

Material. MCNA 9316, from Peñacerrada I amber; fore- and hind wing fragments from the same side of the body and a poorly preserved part of the abdomen, although the genitalia is somewhat visible. The amber piece contains abundant organic remains. The specimen is preserved together with legs of a spider as syninclusions.

Descriptive notes. Male. Small size (inferred from preserved wing fragments). *Forewing.* Length as preserved about 4.5, maximum width not measurable. Two discoidal cells posterior to MP; posterior branch of MP unforked; M-CuA separation not preserved; 2A arcuate. *Hind wing.* Length as preserved about 4.7, maximum width not measurable. Costal field relatively narrow; four c-sc crossveins preserved; Sc ending into C at length of first radial cell's midlength; pterostigma not evidently infumate, not closed basally by a crossvein, at least proximally; first discoidal cell not especially small (or compact) (small in *Cantabroraphidia marcanoi*); rs+ma-mp crossvein present. *Abdomen.* Length as preserved (including genitalia) 3.8. Gonocoxites 9 with paired

basal inner tubercles with small dark teeth; gonocoxites 9 elongate, with very long, stiff setae distally; gonostyli 9 very elongate, slightly upcurved; parameres not conspicuous; tergite 10 (+11?) with distalmost two or three stripes of trichobothria.

Comments. The preserved characters of MCNA 9316 are not enough to create a new taxon. The combined presence of two discoidal cells posterior to MP as in *Cantabroraphidia* and *Amarantoraphidia* gen. n., and the lack of a crossvein closing the pterostigma basally in the preserved wing length as in *Necroraphidia* gen. n., *Ororaphidia*, and *Styporaphidia* (showing three discoidal cells), precludes assignment to any of these genera. The lack of a crossvein closing the pterostigma basally can mean that the base of the pterostigma may have been diffuse or that the pterostigma may have been placed in a more distal position, as occurs in some mesoraphidiids. However, the inferred size of MCNA 9316 would have not been as reduced as in the minute mesoraphidiids but would have better fit with that of those mesoraphidiids with a diffuse pterostigmal base (refer to comments for *Necroraphidia* gen. n.). Furthermore, the presence of a rs+ma-mp crossvein in the hind wing as occurs in MCNA 9316 is a very rare character among described Mesoraphidiidae but more common in modern snakeflies, although it is also present in *S. magia*. The morphology of the genitalia appear distinctive enough as to be recognizable in future findings. It is interesting to note that Aspöck and Aspöck (2004: figs 9, 10) used the presence of wartlike tubercles (covered with dark teeth) on the inner side of gonocoxite 9, larger but similar to those shown by MCNA 9316, as a diagnostic character for the inocelliid genus *Succinofibla* Aspöck & Aspöck, 2004 from Baltic amber. These authors also suggested that these tubercles could be related with the closing mechanism of the genitalia.

Dichotomous keys

The following keys include only those species sufficiently diagnostic to name. As such, the additional morphospecies are not considered here and so all new material should be cross-referenced with the above accounts on those more fragmentarily known taxa. Note that *Alavaraphidia imperterrita* sp. n. is absent from the first key given that the diagnostic parts of the forewings are not preserved.

Key to genera and species of Spanish amber Raphidioptera based on wings

1 Fore-/hind wing with pterostigmal crossvein **2**
– Fore-/hind wing without pterostigmal crossvein (Mesoraphidiidae) **4**
2 Fore-/hind wing with sparse or moderate crossvenation; at most with two radial cells, three medial cells, and three discoidal cells posterior to MP; often with no closed subradial cells (i.e., cells between Rs branches) (Mesoraphidiidae) **3**

– Fore-/hind wing with relatively rich crossvenation; with at least three radial cells, and numerous subradial, medial, and discoidal cells posterior to MP (Baissopteridae) ..... ***Baissoptera? cretaceoelectra* sp. n.**

3 Fore-/hind wing with a single pterostigmal crossvein; distalmost r-rs crossvein meeting R within pterostigma, Rs (proximally) forking before distalmost r-rs; rs-ma crossvein meeting MA before its distalmost fork..... ..... ***Necroraphidia arcuata* gen. et sp. n.**

– Hind wing with two pterostigmal crossveins; distalmost r-rs crossvein meeting R beyond pterostigma, Rs forking at r-rs crossvein; rs-ma crossvein meeting MA after its distalmost fork ..... ***Styporaphidia? hispanica* sp. n.**

4 Forewing with four c-sc crossveins; apicalmost branch of CuA forked near wing margin; M-CuA separation between 1cua-cup and 2cua-cup crossveins (closer to latter)..... ***Cantabroraphidia marcanoi* Pérez-de la Fuente et al., 2010**

– Forewing with six c-sc crossveins; apicalmost branch of CuA unforked; M-CuA separation at the 1cua-cup crossvein .... ***Amarantoraphidia ventolina* gen. et sp. n.**

Key to minute mesoraphidiid amber genera based on non-wing characters

1 Head not rhomboidal; compound eyes shorter, equal, or not much longer than head posterior to eyes; antennae with a low number of flagellomeres (≤ 26) **2**

– Head rhomboidal; compound eyes longer than head posterior to eyes; antennae very elongate, with a high number of flagellomeres (≥ 38) **5**

2 Head ovoid; compound eyes shorter or equal than head posterior to eyes; antennae with less than 26 flagellomeres **3**

– Head quadrangular; compound eyes slightly longer than head posterior to eyes;antennae with 26 flagellomeres .... ***Cantabroraphidia* Pérez-de la Fuente et al., 2010**

3 Compound eyes not distinctly shorter than head posterior to eyes; ocelli positioned between posterior half of compound eyes **4**

– Compound eyes distinctly shorter than head posterior to eyes; ocelli positioned between anterior half of compound eyes ..... ***Amarantoraphidia* gen. n.**

4 Compound eyes nearly equal than head posterior to eyes; antennae longer than head length; posterior border of head without a collar-like lip .... ***Nanoraphidia* Engel, 2002**

– Compound eyes apparently slightly longer or equal than head posterior to eyes; antennae shorter than head length; posterior border of head with a collar-like lip ..... ***Grimaldiraphidia* Bechly & Wolf-Schwenninger, 2011**

5 Compound eyes two times head posterior to eyes; clypeus short; antennae with around 38 flagellomeres; pronotum longer than head; bilobed extensions of third tarsomere lacking digitiform processes..... ..... ***Lebanoraphidia* Bechly & Wolf-Schwenninger, 2011**

– Compound eyes ca. 1.4 times head posterior to eyes; clypeus especially elongate; antennae with more than 38 flagellomeres; pronotum shorter than head; bilobed extensions of third tarsomere with distal digitiform processes..... ..... ***Alavaraphidia*** **gen. n.**

Discussion

Taxonomy

Recently, Bechly and Wolf-Schwenninger (2011) transferred several species of *Mesoraphidia* to the genus *Grimaldiraphidia*. Based on their study, these transfers were made to eliminate the putative paraphyly of *Mesoraphidia*, and the referred species were claimed to share the synapomorphic characters the authors used for their tribe Nanoraphidiini Bechly and Wolf-Schwenninger, 2011 (although recognition of this tribe leaves the remainder of their Mesoraphidiinae paraphyletic), i.e, "Rs distally unbranched or only with single apical fork, [ptero]stigma very long, postorbital margin region of head shortened, ovipositor short and conspicuosly strong (?), minute size of body and wings". While at least those few wing characters are correct for the combinations *G. mitchelli*, *G. parvula*, and *G. purbeckensis*, the transference of *M. durlstonensis* Jepson, Coram and Jarzembowski, 2009 and *M. heteroneura* Ren, 1997 to *Grimaldiraphidia* is in stark contradiction with some of these, as the holotype of *M. durlstonensis* has a forewing 10.6 long (Jepson et al. 2009), whereas *M. heteroneura* has a forewing with Rs forked twice and 10.5 long (Ren 1997). Moreover, the combination *Yanoraphidia gaoi* Ren in Ren et al., 1995 was restored in Pérez-de la Fuente et al. (2010) (it was previously transferred to *Mesoraphidia* by Engel in 2002) based on the distinctive pterostigma that goes up to the apex of R. By this reasoning, the transfer of this species by Bechly and Wolf-Schwenninger (2011) from the genus *Mesoraphidia* to the genus *Grimaldiraphidia* is not valid nor necessary. Accordingly, we formally return *M. gaoi* to *Yanoraphidia* (as done by Pérez-de la Fuente et al. 2010), and *G. durlstonensis* and *G. heteroneura* to *Mesoraphidia*, restoring the combinations *Yanoraphidia gaoi* Ren in Ren et al., 1995 stat. rest., *Mesoraphidia durlstonensis* Jepson, Coram and Jarzembowski, 2009 stat. rest., and *Mesoraphidia heteroneura* Ren, 1997 stat. rest. While we acknowledge that these last two species should perhaps be placed in a new genus on their own, if the criteria of Bechly and Wolf-Schwenniger (2011) were followed, herein we prefer to take a conservative stance as the genus *Mesoraphidia* is in need of serious revision and further subdivision or changes should be done in the context of such a comprehensive study.

Xylophilous mesoraphiidids

Seven larval mesoraphidiids have been described up to now from five Cretaceous amber localities around the world (Table 2). This circumstance contrasts with the lack

of larval records as compressions, mostly due to the decreased fidelity of preservation of the soft body tissues in such deposits. Taking into account that the larval record of the remainder of holometabolous orders is similarly not that abundant in Cretaceous ambers, the relatively high number of larval mesoraphidiids most likely indicates that at least some, if not all, were corticolous, i.e., they lived under bark, as is well known in extant snakeflies (Aspöck 2002). Therefore, one would expect that this ecological proximity to the resin sources, in addition to their active predatory behaviour, would have greatly increased the chances of larval mesoraphidiids to become embedded in resin. This inference is reinforced by the ovipositor structure in *Amarantoraphidia ventolina* sp. n. and *Alavaraphidia imperterrita* sp. n. Both show a dense annulation along the entire ovipositor (Fig. 7C), as occurs in Recent snakeflies (Mickoleit 1973), and which is an adaptation suitable for laying eggs deep inside irregular surfaces such as bark crevices. Today, whereas all known larval Inocellidae are corticolous, a significant number of Raphidiidae are terricolous as immatures, living in superficial layers of soil or detritus at the base of trees or shrubs (Aspöck 2002). The fact that the adult holotypes of *Cantabroraphidia marcanoi*, *Necroraphidia arcuata* sp. n., and *A. ventolina* have associated timber debris as syninclusions (especially abundant in the amber piece containing *C. marcanoi*, Fig. 12), most likely indicates xylophilous activity.

Uniqueness of the Spanish amber snakefly fauna

Like many moderate- to large-sized insects, snakeflies are difficult to find as amber inclusions, particularly complete specimens in Cretaceous ambers. It is not surprising that those individuals recovered as complete, or relatively complete, inclusions are among the smallest members of the order. Nonetheless, immatures and fragments of much larger snakefly species are also found as amber inclusions as evidenced by the rich Spanish fauna. What is more curious is that among the more abundant Cretaceous amber sources such as Lebanon, Myanmar, New Jersey, and Canada, the reported snakeflies remain relative rarities (Table 2; Engel pers. obs.), and the fragmentary remains of numerous, sometimes larger, species that are observed in the Spanish deposits are not seen in these other outcrops. Why should the Iberian fauna be so particularly rich? It is similarly enigmatic that as of yet the younger French ambers (late Albian to Cenomanian), with the exception of two larval head capsules from the late Albian Archingeay - Les Nouillers outcrop in southwestern France (Perrichot and Engel 2007), have not yielded significant raphidiopteran specimens despite the close geographic proximity of the sources. This dramatic faunal difference is seen in other groups. For example, ants are relatively diverse in French amber, but entirely absent in Spanish amber, while stigmaphronid wasps are most diverse in Spanish amber but missing from the deposits of France (Ortega-Blanco et al. 2011). These faunal singularities might have been caused by the insularity that the Iberian Plate had from the Early Jurassic to the Late Cretaceous (see Blakey 2011). However, whether these contrasting faunas are just a result of localized environmental differences or the younger age of the French deposits is not

entirely clear. The difference in age is not that great and given the similarities in some of the ant taxa between French and Burmese ambers, it is peculiar that there should not be greater similarity between the French and Spanish amber faunas. Furthermore, the amber of Archingeay - Les Nouillers, which is the richest French amber deposit from the Cretaceous, seems to be sampling a more litter fauna (Perrichot 2004), so it is plausible that in that particular case these observed faunal differences, to a greater or lesser extent, could be taphonomic in origin.

However, another hypothesis could explain the high abundance/diversity of snakeflies in Spanish amber, apart from its insularity. Perhaps this abundance is partly owing to the common occurrence of wildfires in the Spanish amber environment, inferred from evidence at several Spanish amber localities (see Najarro et al. 2010). The evidence of abundant charcoal associated with the Spanish ambers, the abundant amber masses with charcoalified plant fibers as inclusions (e.g., Fig. 4A), and the presence of gleicheniacean ferns remains, the last of which are primary succession pioneers following wildfires. After wildfires, there is abundant timber available for xylophagous or xylophilous insects, and resin production among surviving trees is greatly increased (e.g., Grimaldi 2000, Moretti et al. 2006, McKellar et al. 2011, Santolamazza-Carbone et al. 2011). As has been pointed out above, it seems most likely that mesoraphidiids had a xylophilous biology, adults laying their eggs under or in bark crevices (including dead timber), and both immatures and adults assuredly predators of xylophagous or xylophilous arthropods (analogous to living species which predate tree or shrub inhabiting insects). Thus, the combination of a xylophilous biology of adult and immature snakeflies and periodic wildfires might together result in greater resources for these species and at the same time a higher probability of them becoming ensnared in the increased resin flows. *Necroraphidia arcuata* and *Amarantoraphidia ventolina* are actually preserved with charcoalified plant fibers as syninclusions (see Figs 4A, 7A; Pérez-de la Fuente et al. 2012), highlighting that they were entrapped after an episode of burning. Nevertheless, wildfires seem unable to explain entirely the richness of the Spanish snakefly paleofauna, as these would have also been involved in the origin of the Turonian amber accumulation from New Jersey (Grimaldi et al. 2000).

Conclusions

The discovery of the first amber baissopterid is especially remarkable. Furthermore, the presence of the family in the Iberian territory during the Early Cretaceous completes the remarkable preexisting paleogeographic baissopterid hiatus between the Cretaceous localities from eastern Asia and Brazil.

With the fossils herein described, the Albian amber of Spain currently harbors the greatest abundance and diversity of snakeflies in Cretaceous resins. As is also suggested by other paleoentolomological records, this significant snakefly paleodiversity may reflect a faunistic singularity of the Iberian territory during the Albian perhaps as a consequence of its geographic isolation during the Jurassic and the Cretaceous, or a

combination of this with an environment resulting from episodic wildfires. Wildfires would have increased the availability of dead wood as a substrate for the xylophagous or xylophilous insects to develop, which, in turn, could have aided the increase in the xylophilous, predatory snakefly populations.

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Anexo I.7

Description of the male of Megalava truncata *Perrichot, 2009 (Hymenoptera: Megalyridae) in Early Cretaceous Spanish amber from El Soplao*

Descripción del macho de *Megalava truncata* Perrichot (Hymenoptera: Megalyridae) en ámbar del Cretácico Inferior de El Soplao (España)

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Resumen:

Se describe un nuevo fósil de avispa megalírida recientemente descubierto en ámbar del Cretácico Inferior (Albiense) de El Soplao (Cantabria, España). El nuevo fósil se considera el macho de *Megalava truncata* Perrichot, 2009, originalmente descrito del ámbar de Peñacerrada I (= Moraza; Burgos, España). El nuevo espécimen permite una descripción más completa del género *Megalava*, el cual se estableció originalmente basado en un único espécimen fragmentario, carente del metasoma. Además, el nuevo espécimen ha permitido revisar los caracteres con valor filogenético para el clado [*Megazar* + *Megalava*].

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Description of the male of *Megalava truncata* Perrichot (Hymenoptera: Megalyridae) in Early Cretaceous amber from El Soplao (Spain)

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Abstract

A new fossil of megalyrid wasp recently discovered in Early Cretaceous (Albian) amber from El Soplao (Cantabria, Spain) is described as the male of *Megalava truncata* Perrichot, 2009, originally described from Peñacerrada I (= Moraza) amber (Burgos, Spain). The new specimen permits a more thorough description of the genus *Megalava*, which was established originally from a single, fragmentary specimen lacking the metasoma, and also permits a discussion on the characters of phylogenetic value for the clade [*Megazar* + *Megalava*].

Key words: Mesozoic, amber, wasps, Megalyroidea, taxonomy, Spain

Introduction

Studies on Megalyridae, or long-tailed wasps, have gained a significant shift in the last years with the record of several extinct and extant taxa from the Northern Hemisphere (Perrichot 2009; Mita *et al*. 2007; Mita & Konishi 2011), while former knowledge essentially revealed a Southern Hemisphere distribution. Whereas the family currently comprises 51 Recent species segregated into eight genera, principally distributed in tropical areas of the Southern Hemisphere and around the equator, but also present in Southeast Asia and Japan, the fossil record shows 13 species in one Recent and six extinct genera ranging from the Early Cretaceous (Albian) to the Eocene (see Vilhelmsen *et al*. 2010a). The biology of Megalyridae remains poorly understood but the few observations of some species of *Megalyra* suggest they are mostly idiobiont parasitoids of immature stages of beetles and more rarely sphecid wasps (Naumann 1987; Shaw 1990), both of which are found in Spanish ambers (Peñalver & Delclòs 2010).

Phylogenetic analyses including the recent findings support sister-group relationships of Megalyroidea (comprising the sole Megalyridae) with Ceraphronoidea (Vilhelmsen *et al*. 2010a), a hypothesis followed by several other studies (Gibson 1985; Sharkey 2007; Vilhelmsen *et al*. 2010b; Vilhelmsen 2011; Sharkey *et al*. 2012) while a few works suggest relationships with Trigonalyoidea (Davis *et al*. 2010; Heraty *et al*. 2011). The mesothoracic spiracle exposed in the upper corner of the pronotum and completely surrounded by pronotal cuticle has been suggested as a synapomorphy shared with Ceraphronoidea (Gibson 1999), though in *Megazar* Perrichot, 2009 the pronotal cuticle forms a posterior notch making the spiracle free posteriorly (Perrichot 2009: fig. 16.3). However, contrasting results arise from the absence of a clear set of autapomorphies, as megalyrids are recognized by an unique combination of characters otherwise found individually in some other hymenopteran families (see discussion in Vilhelmsen *et al*. 2010a): (1) the antennae inserted below the ventral margin of the compound eyes, (2) well-developed subantennal grooves, (3) a flat mesoscutum longitudinally divided by a median mesoscutal sulcus

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(but absent in *Carminator* Shaw, 1988), (4) the absence of notauli, that was proposed as a megalyrid groundplan feature by Vilhelmsen *et al*. (2010a), and (5) large triangular axillae normally abutting in the middle.

Two monotypic genera of long-tailed wasps have been described from Early Cretaceous (Albian) Spanish amber of Peñacerrada I, namely *Valaa* Perrichot, 2009 and *Megalava* Perrichot, 2009, the latter based on an incomplete specimen (Perrichot 2009). A new, complete specimen assignable to *Megalava truncata* Perrichot, 2009 has been discovered in contemporaneous amber from the El Soplao outcrop in Rábago (Cantabria, Spain. See Najarro *et al*. 2009, 2010). The discovery of this specimen permits us to provide a revised diagnosis for the genus and a more complete account of the species.

Material and methods

The specimen is housed in the Institutional Collection from the El Soplao outcrop in the Laboratory of the El Soplao Cave, Celis, Cantabria (Spain). The fossil is preserved in a polished piece of amber, which has been embedded in a clear, synthetic block of epoxy resin according to the method of Corral *et al*. (1999) and Nascimbene & Silverstein (2000).

Photomicrographs were prepared using a Nikon D1x digital camera attached to an Infinity K-2 long-distance microscope lens, whereas drawings and measurements were made with an Olympus BX51 microscope equipped with a camera lucida and an ocular micrometer. Photographs were merged using CombineZ5 software.

Morphological terminology follows that used by Perrichot (2009) unless otherwise noted. Abbreviations used in the text and figures are: A, anal vein; C, costal vein; Ce, cercus; Cu, cubital vein; M, medial vein; *m*, medial cell; *mrg*, marginal cell; Pt, pterostigma; R1, radial vein 1; Rs, radial sector; *sbmrg*; submarginal cell; T9/10, tergite 9 or 10 (apicalmost visible tergite); V, volsellae.

Other material examined: *Megalava truncata*; holotype MCNA-9416, from Peñacerrada I amber (Albian), Burgos Province, Spain; *Megazar elegans*, holotype MNHN-CDL-2.11, from Charentes amber (late Albian), France.

Systematic Paleontology

Family Megalyridae Schletterer, 1889

Tribe Megazarini Perrichot, 2009

Genus *Megalava* Perrichot, 2009

Megalava Perrichot, 2009: 25, fig. 17. Type species: *Megalava truncata* Perrichot, 2009, by original designation [from Albian of Peñacerrada I (= Moraza), Burgos, Spain].

Revised diagnosis. The genus is distinctive from *Megazar*, the only other genus presently included in the tribe, in (1) having a longitudinal median sulcus on the vertex, (2) the occipital carina foveate, (3) the parapsidal lines running nearly parallel to the median mesoscutal sulcus, (4) the scutoscutellar sulcus (*sensu* Vilhelmsen *et al*. 2010b) broadly crenulate, (5) M and Cu entirely tubular, (6) the medial cell rectangular instead of pentagonal.

Megalava truncata Perrichot, 2009
(Figs 1−2)

Material. Male, CES 391.2, from Early Cretaceous (Albian) El Soplao amber (Cantabria, Spain). The specimen is almost complete, missing only the distal parts of some legs. Its preservation is generally good but the head and the anterior part of mesosoma are surrounded by cracks, rendering it difficult to observe the longitudinal median sulcus of vertex, the clypeus shape, and mandibular teeth. In addition, the piece of amber also contains abundant syninclusions: two coiled charcoalified plant fibers (Fig. 1A; see Najarro *et al*. 2010: fig. 7.1) in contact with the right

antenna of the megalyrid, a new genus and species of snakefly (Pérez-de la Fuente *et al*. in prep.), two coleopterans, another hymenopteran, one immature aphid, a cluster of trichomes, and some other indeterminate organic remains. The syninclusions prevent polishing from either side of the preparation and limit the dorsal observation of the megalyrid, so the hind wing venation is not discernible and measurements of the width of the body are not possible.

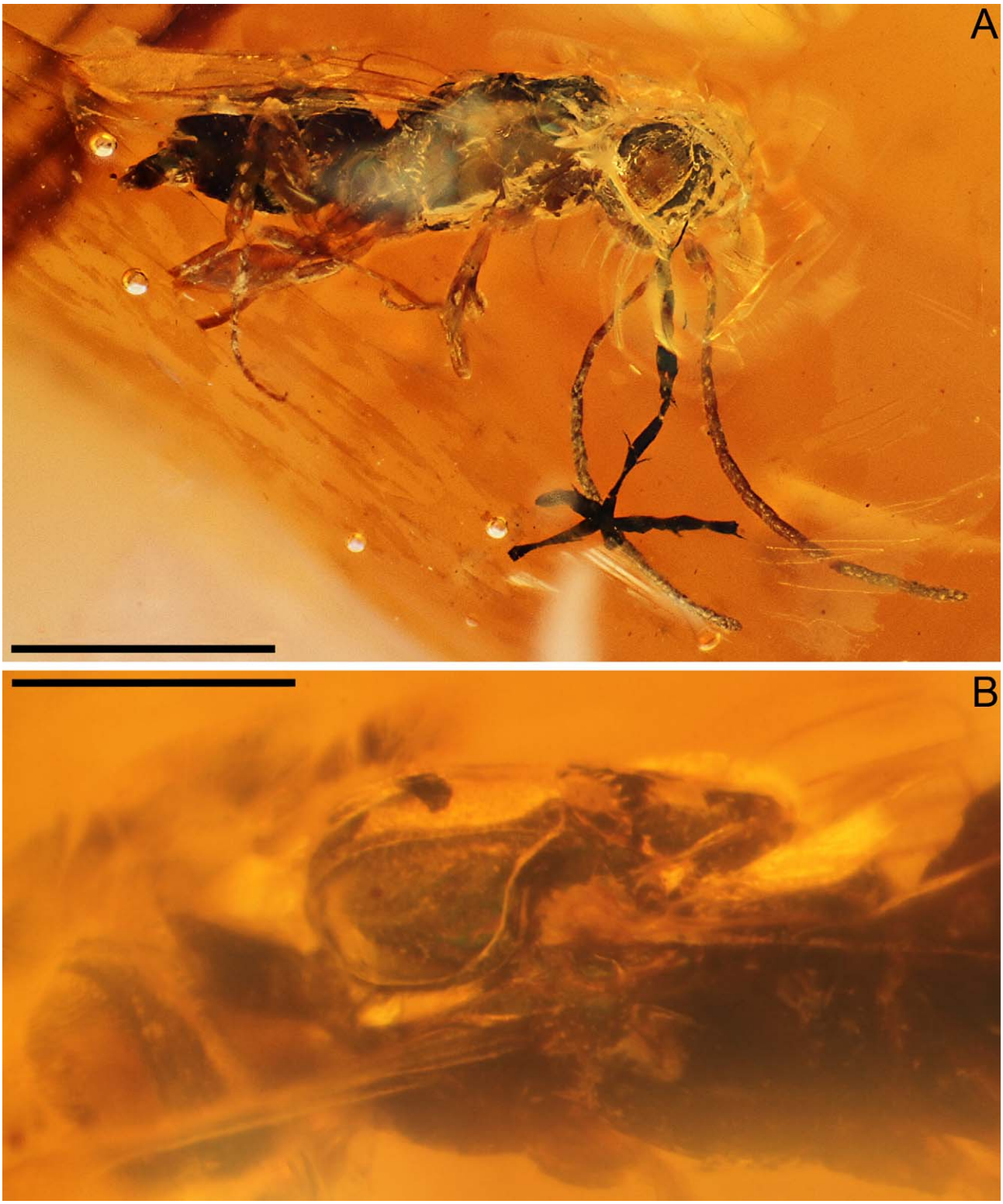

FIGURE 1. Photomicrographs of *Megalava truncata* Perrichot, 2009, new specimen CES 391.2 from El Soplao amber, male. A, lateral habitus; B, detail of mesosoma. Scale bars: A = 1 mm, B = 0.5 mm.

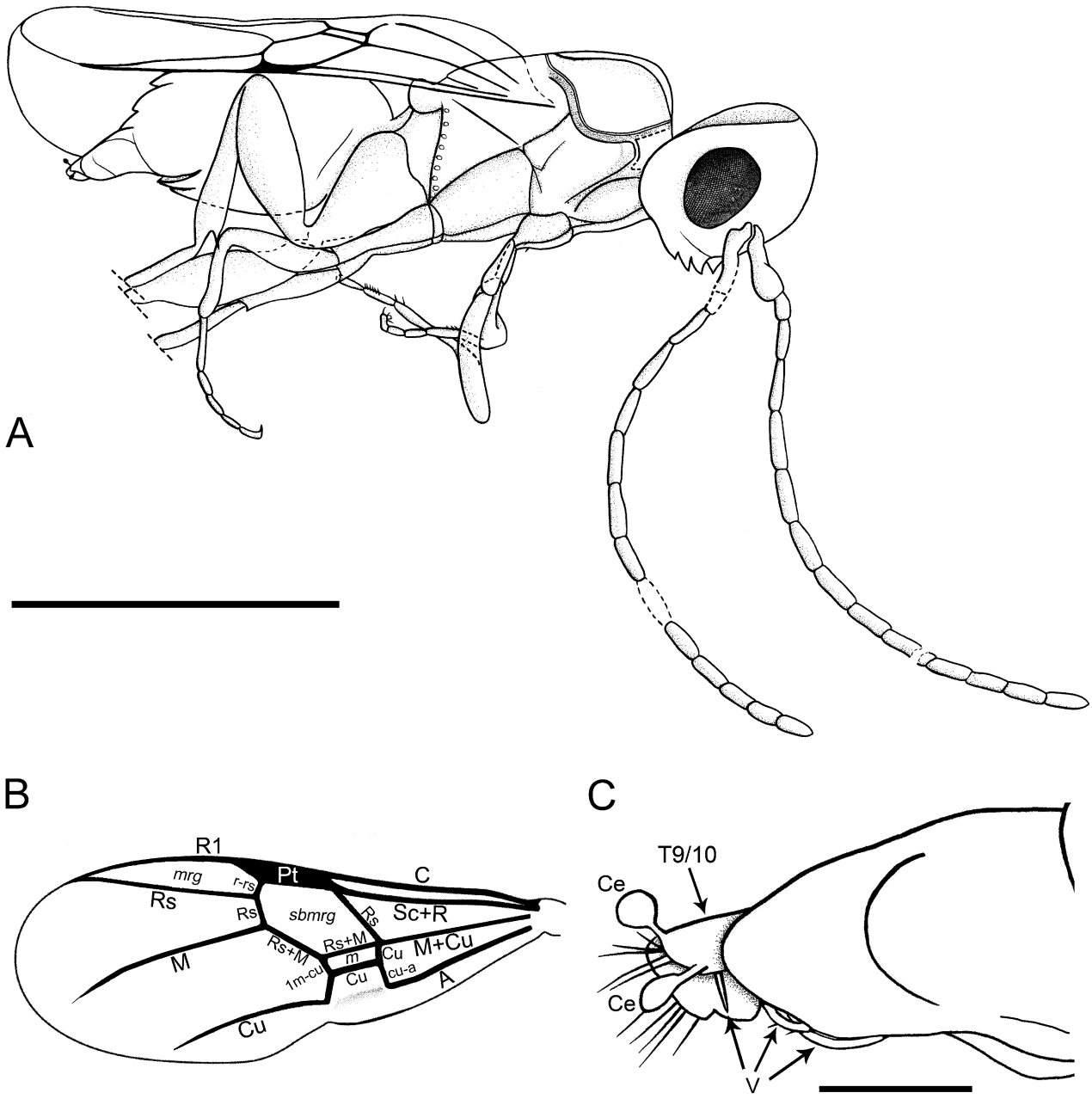

FIGURE 2. Line drawings of *Megalava truncata* Perrichot, 2009, new specimen CES 391.2 from El Soplao amber, male. A, camera lucida drawing, lateral habitus; B, diagrammatic illustration of forewing reconstruction; wing width has been estimated; C, camera lucida drawing of the genitalia in lateral view. Scale bars: A, B = 1 mm, C = 0.1 mm.

Description. *Head*. Shorter than wide and shorter than high, likely broader than mesosoma. Compound eyes higher than long, not pubescent; postorbital margin without groove, foveae, or carina. Relative distance between lateral ocelli not visible, lateral ocelli almost aligned with the posterior margin of compound eyes. Occipital carina foveate. Antenna elongate; toruli closer to each other than to compound eyes; pedicel half as long as scape, scarcely longer than broad; flagellomeres cylindrical; FIX–XII shortest, scarcely twice as long as thick; FI, FV–VIII about three times as long as thick; FII–IV longest, about four times as long thick. Right mandible as visible with one small basal tooth and two larger apical teeth; left mandible with one large apical tooth visible.

Mesosoma (Fig. 1B). Anteromedial part of pronotum only slightly visible dorsally; presence of notch on hind lateral margin of pronotum not clear. Mesoscutum abruptly truncate anteriorly, with strong anterolateral carina, and with posterior margin not straight dorsally; median mesoscutal sulcus distinct, not crenulate; parapsidal lines well impressed, widely separated from median mesoscutal sulcus and running nearly parallel to it. Axillae large, slightly

meeting at medial angles anteriorly, with scutoscutellar sulcus broadly crenulate. Mesoscutellum acute posteriorly, without a transversal sulcus. Mesometapectal sulcus (*sensu* Vilhemsen et al. 2010b) foveolate. Posterior margin of metapleuron foveolate. Propodeum with sharp angle between dorsum and almost vertical posterior surface.

Wings (Fig. 2B). Membrane hyaline, with microtrichia. Forewing exceeding posteriorly the tip of the metasoma; pterostigma relatively elongate (slightly longer than medial cell); vein R1 long, almost reaching wing apex; Rs present between r-rs and Rs+M forming a large submarginal cell, apical segment of Rs straight and tubular, reaching wing margin; M+Cu tubular, aligned with Rs+M; marginal and submarginal cells closed by tubular veins, marginal cell narrow and elongate; medial cell subrectangular, very small, entirely closed by tubular veins, with 1m-cu very short and slightly oblique; distal parts of M and Cu tubular, almost reaching wing margin.

Legs. Foreleg with preening brush of stiff, short setae visible on inner margin of tarsomeres; hind leg stout, with large coxa; metafemur swollen, without comb-like spines along inner margin; metatibia with two short apical spurs, without comb-like spines along inner margin; pretarsal claws small, simple, with an almost equally sized arolium.

Metasoma. Ovoid, not especially elongate (less than half the body length). Tip of genitalia with tergite 9/10 visible, bearing two well-developed spatulate structures interpreted as cerci and some long and very fine setae; volsellae visible, bearing a few minute, short setae; parameres straight, poorly developed, ending at same level as T9/10 (Fig. 2C).

Measurements (in mm). Body length 2.30; head length 0.35, height 0.67; antenna length 1.88; mesosoma length 0.80; forewing length 1.65; metasoma length 1.02.

Discussion

The specimen described here clearly belongs in the clade [*Megazar* + *Megalava*], i.e. the tribe Megazarini, which is characterized by the following characters (see Perrichot 2009): (1) the large mesoscutum with parapsidal lines, (2) the forewing with vein M+Cu tubular, (3) the basal segment of Rs very long, and (4) the marginal cell enclosed and narrow. Another important character of the Megazarini also proposed by Perrichot (2009) was the presence of comb-like spines on the inner margin of the metatrochanter, metafemur, and metatibia. Only this character and the character (2) supported this clade (Vilhelmsen *et al*. 2010a). But whereas comb-like spines are present in the female of *Megazar* and the holotype of unknown sex of *Megalava*, they are absent in the new male specimen. Hence, additional Cretaceous material will be necessary to clarify if this is a species-specific character or a sexually dimorphic trait present only in females (as a grooming device?).

Other characters also proposed by Perrichot (2009) to define the Megazarini were tentative because they were clearly visible only in *Megazar*, i.e. the mandibles broad and short, with four teeth, the mesothoracic spiracle free posteriorly, and the hind wing venation reduced to Sc+R. Unfortunately, these characters are still not elucidated with the new specimen as preserved, which otherwise displays most diagnostic characters of the holotype of *M. truncata* as described by Perrichot (2009): the occipital carina foveate, the scutoscutellar sulcus broadly crenulate, and the forewing with a small and rectangular medial cell and apical parts of veins M and Cu tubular. It also differs from *Megazar* by its parapsidal lines running nearly parallel to the median mesoscutal sulcus, whereas these lines strongly diverge anteriorly in *Megazar*.

In addition to the absence of comb-like spines on the hind leg, three differences can be observed in the new specimen from El Soplao compared with the holotype of *M. truncata* (see Perrichot 2009: fig. 17): (1) the mesoscutum is bordered anterolaterally by a carina in the new specimen contrary to what was described from the holotype (but this part is scarcely visible in the holotype); (2) the parapsidal lines run along the entire mesoscutal length in the new specimen while they are short in the holotype, visible only in the posterior part (but the right parapside is distinctly longer than left one in the holotype, so this can be confidently regarded as of preservational origin); and (3) foveolae are apparently absent along the mesometapectal sulcus in the holotype contrary to what occurs in the new specimen (but, again, this part is scarcely visible in the holotype). Since these differences most likely result from preservation and one is equivocal whether it is sexually dimorphic or not, we consider them as not robust enough to justify a separate species, and we prefer to adopt a conservative approach, considering the present specimen as the male of *M. truncata* until further findings can definitely indicate if the spines on hind legs are a dimorphic character or not.

This is the third occurrence of an insect species in amber from Peñacerrada I and El Soplao, both located in the Basque-Cantabrian Basin in northern Spain. Also known from both localities are the mymarommatid *Archaeromma hispanicum* Ortega-Blanco *et al*., 2011 and the ceratopogonid *Protoculicoides skalskii* Szadziewski and Arillo, 1998 (the latter being found also in amber from the San Just outcrop in Teruel, Spain) (Szadziewski & Arillo 1998; Arillo *et al*. 2008; Ortega-Blanco *et al*. 2011; Pérez-de la Fuente *et al*. 2011). Whereas this paleoentomological evidence further indicates a similar age for these two Spanish Albian amber localities, the geological and paleobotanical data indicates paleoenvironmental differences between both localities, with more marine influence in El Soplao than in Peñacerrada I and some floristic discrepancies (Najarro *et al*. 2010; Peñalver & Delclòs 2010).

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Anexo I.8

A new species of the diverse Cretaceous genus Cretevania *Rasnitsyn, 1975 (Hymenoptera: Evaniidae) from Spanish amber*

Una nueva especie del género cretácico diverso *Cretevania* Rasnitsyn, 1975 (Hymenoptera: Evaniidae) del ámbar de España

Referencia completa:

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Resumen:

Se describe *Cretevania soplaensis* nov. sp. del ámbar del Cretácico Inferior (Albiense) de El Soplao (Rábago, Cantabria, norte de España). Aunque el espécimen estudiado está incompleto, sus partes preservadas permiten distinguirlo del resto de especies previamente descritas. Se incluye una discusión sobre un dimorfismo sexual probable en el género *Cretevania* y sus posibles consecuencias para la identificación de nuevas especies basadas en especímenes de sexo desconocido o incierto.

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A new species of the diverse Cretaceous genus *Cretevania* Rasnitsyn, 1975 (Hymenoptera: Evaniidae) from Spanish amber

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Abstract

Cretevania soplaensis nov. sp. is described from the Early Cretaceous (Albian) amber from El Soplao (Rábago, Cantabria, northern Spain). Although the studied specimen is incomplete, its preserved parts permit us to distinguish it from the previously described species. A discussion about probable sexual dimorphism in *Cretevania* and possible consequences for the identification of new species based on specimens of unknown or uncertain sex is included.

Key words: ensign wasps; new taxon; amber; Albian; Spain

Introduction

Evaniidae (ensign wasps), one of the three extant families of the superfamily Evanioidea, are cosmopolitan hymenopterans, mainly present in the tropic, and parasitoids of cockroach eggs (Dictyoptera) within oothecae (Deans & Huben 2003; Grimaldi & Engel 2005; Deans 2005). Up to now, eight Mesozoic genera of Evaniidae are known, plus the genera *Praevania* Rasnitsyn, 1991 and *Andrenelia* Rasnitsyn & Martínez-Delclòs, 2000 if they are considered evaniids (Peñalver *et al.* 2010). Currently, only one fossil family is included in the Evanioidea with confidence, the family Praeaulacidae (Rasnitsyn 1972), although the validity of Andreneliidae (Rasnitsyn & Martínez-Delclòs 2000) as a separate family remains uncertain (Basibuyuk *et al.* 2002; Grimaldi & Engel 2005; Zhang & Rasnitsyn 2007, 2008). Peñalver *et al.* (2010) provides an updated discussion on the phylogeny of the superfamily Evanioidea. The updated extant and fossil evanioid taxa are available in Deans *et al.* (2012) and Jennings *et al*. (2012).

The most diverse fossil evanioid genus is *Cretevania*, established by Rasnitsyn (1975) and currently a member of the family Evaniidae. *Cretevania* is mainly characterized by its reduced forewing venation and the shape of the hind legs and petiole. Up to now, 13 species of this genus are known from different Cretaceous deposits of amber and compression rocks from Eurasia and the Middle East, the highest diversity being known from Spain as was indicated by the study of abundant material from Early Cretaceous amber present in different localities of this country (Peñalver *et al.* 2010).

A cladistic analysis of fossil and extant members of the superfamily Evanioidea, a summary of the fossil record of the family Evaniidae, a review of the genus *Cretevania* (including an emended diagnosis of the genus), the re-study of the Russian holotypes, the reinterpretation of two Cretaceous genera synonymized with *Cretevania*, and the description of four new species from Spanish amber were provided by Peñalver *et al.* (2010). In addition, this last study of fossil evaniids included a review of the paleogeographical and stratigraphical occurrences of the genus.

The present contribution expands the knowledge of the diverse Cretaceous genus *Cretevania* by describing a new species found in a recently discovered Early Cretaceous amber locality from northern Spain.

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Geological setting

The El Soplao outcrop is located at the north-west margin of the Basque-Cantabrian Basin. The development of the basin during the Early Cretaceous is related to the kinematics between the European and Iberian plates (Olivet 1996). The El Soplao amber-bearing deposit, Albian in age, is included within the Las Peñosas Formation, in a unit of heterolithic sandstones-siltstones and carbonaceous mudstones related to broadly coastal delta-estuarine environments (Najarro *et al.* 2009). Amber occurs in a level of organic-rich clays, which also contains abundant plant cuticles mainly belonging to cheirolepidiaceans and ginkgoaleans. Preliminary data on palynology and extensive taphonomical evidences to reconstruct the origin of this deposit are provided by Najarro *et al*. (2010). Peñalver & Delclòs (2010) provided a general context of the Spanish amber deposits, including the El Soplao outcrop.

Material and methods

The amber piece containing the studied specimen was embedded in epoxy resin for better observation and preservation, as described in Corral *et al*. (1999) and Nascimbene & Silverstein (2000).

Wing venation terminology follows that used in Peñalver *et al.* (2010), which, in turn, follows that of Deans & Huben (2003) and includes other morphological terminology of Huber & Sharkey (1993) and convention for names of vein intersections by Louis (1971). In order to calculate the pterostigmal and wing cell ratios: 1) the pterostigmal length has been measured from the pterostigmal proximal margin to its meeting with the 1r-rs crossvein, as done by Peñalver *et al*. (2010); 2) the first submarginal cell maximum width has been perpendicularly measured from Sc+Rb to the point of divergence between 2RS and 2M; 3) the first marginal cell maximum width corresponds to the basal (subbasal for some species) width of the cell, and has been perpendicularly measured from the separation between 3RS and 4RS (or, if not distinct, the very beginning of 3RS+4RS) to the outer edge of the pterostigma.

Drawings were prepared with a camera lucida attached to an Olympus BX51 microscope. Photomicrographs were taken using a digital camera ColorView IIIu attached to an Olympus BX51 microscope.

Systematic Paleontology

Order Hymenoptera Linnaeus, 1758

Suborder Apocrita Gerstaecker, 1867

Family Evaniidae Latreille, 1802 (as Evaniales)

Genus *Cretevania* Rasnitsyn, 1975

Type species. *Cretevania minor* Rasnitsyn, 1975 from Late Santonian Yantardakh amber (Taimyr, Russia; see Zherikhin & Eskov 1999).

Other species included. *Cretevania concordia* Rasnitsyn, Jarzembowski & Ross, 1998 from the Late Hauterivian Clockhouse Brickworks compression locality (England); *C. cyrtocerca* (Deans *et al.*, 2004) from the Neocomian-Lowermost Aptian Mdeyrij-Hammana amber locality (Lebanon); *C. meridionalis* Rasnitsyn, 1991 from the Barremian-Early Aptian? Bon-Tsagan-Nur compression locality (Mongolia); *C. pristina* (Zhang & Zhang, 2000), *C. exquisita* (Zhang, Rasnitsyn, Wang & Zhang, 2007), and *C. vesca* (Zhang, Rasnitsyn, Wang & Zhang, 2007) from the Barremian−Early Aptian? Beipiao compression locality (Liaoning Province, China); *C. alonsoi* Peñalver, Ortega-Blanco, Nel & Delclòs, 2010 from the Albian Peñacerrada I amber locality (Burgos Province, Spain); *C. montoyai* Peñalver, Ortega-Blanco, Nel & Delclòs, 2010 and *C. alcalai* Peñalver, Ortega-Blanco, Nel & Delclòs, 2010 from the Albian San Just amber locality (Teruel Province, Spain); *C. rubusensis* Peñalver, Ortega-Blanco, Nel & Delclòs, 2010 from the Albian Arroyo de la Pascueta amber locality (Teruel

Province, Spain); *C. minuta* Rasnitsyn, 1975 from the Cenomanian Agapa amber locality (Taimyr, Russia); and *C. major* Rasnitsyn, 1975 from the Late Santonian Yantardakh amber locality (Taimyr, Russia). For a paleogeographic map with the occurrences of *Cretevania* species see Peñalver *et al*. (2010). Note: in the original description of the species *C. rubusensis* there is a double erratum because the holotype number was referred as CPT-2260 in the holotype data section and as MPZ 99/135 in its two figure captions. The actual accession number for the holotype is CPT-3335.

***Cretevania soplaensis* Pérez-de la Fuente, Peñalver & Ortega-Blanco, nov. sp.**
(Figs 1−3)

Holotype. CES 364.2, housed at the Institutional Collection from the El Soplao amber outcrop located in the laboratory of the El Soplao Cave, Celis, Cantabria (Spain). The amber piece is 16 x 9 x 6 mm in size embedded into an epoxy prism of 23 x 15 x 6 mm. The specimen is incomplete, lacking half of the head, part of the left forewing, one hind wing, and the ventral half of the mesosoma including all the legs. The metasoma is very well preserved. The specimen is infested by fungal mycelia. The following syninclusions are preserved together with the holotype: the mesoraphidiid *Amarantoraphidia ventolina* Pérez-de la Fuente *et al.*, 2012 (Pérez-de la Fuente *et al.* 2012), three hymenopterans, four dipterans (one chimeromyiid among them), one thysanopteran, a few fusinite fragments, and a few timber debris, as well as other indeterminate organic remains. This assemblage of syninclusions lacks deformation due to tectonic processes.

Diagnosis (*male*) [See Table 1 for character comparison]**.** Small *Cretevania* species distinguished from the other species within the genus by a flagellum broader distally, a petiole 7.2 times longer than wide, and the following combination of forewing characters: (1) pterostigma 3 times longer than wide, (2) first submarginal cell ca. 4 times longer than wide, (3) vein 2RS nearly straight (i.e., not convex subbasally), (4) first marginal cell 2 times longer than wide at base, (5) 1CU with the same length than 1m-cu, (6) 1r-rs straight (i.e., not concave), arising near the pterostigma apex, (7) vein rs-m spectral, (8) track of rs-m nearly continuous with 1r-rs (slightly distal), (9) vein 2M nearly straight (i.e., not concave subbasally), (10) vein 2CU+3CU steeply changing its slope distally, (11) vein 2cu-a strongly angled towards wing base and track not continuous with 1m-cu, and (12) wing apex rounded (i.e., not pointed).

Etymology. Named after El Soplao, the name of the amber-bearing locality where the holotype was found.

Description (*male*). Estimated length 3.00 mm. Head antero-posteriorly compressed in lateral view, 0.58 long, 0.28 high, width not measurable. Mandible not preserved. Preserved labial or maxillary palpomere 0.12 mm long. Antenna with 11 flagellomeres; flagellum 0.78 mm long, broader distally, cylindrical in section (Fig. 2). Scape apparently elongate, not measurable. Pedicel with a constant width along all its length, 0.07 mm long, 0.04 mm wide, as long as flagellomere I. Flagellomeres I and II similar in length, flagellomere XI acuminate distally and slightly longer than preceding flagellomeres.

Mesosoma features largely obscured. Propodeum with large polygonal reticulated sculpture. Wings hyaline, with abundant microtrichia. Forewing features, apart of the above diagnosed, are as follows (Fig. 1). Greatest width ca. 0.66 mm. Wing veins 2M, 3M, and 2CU+3CU tubular. Vein 2CU+3CU extending to wing margin and arising directly from 1CU. Pterostigma 0.18 mm long, 0.06 mm wide, parallel-sided. Vein 3RS+4RS straight. Vein 1RS not conspicuous, likely nebulous. First discal cell nearly squared. Vein 1m-cu aligned with 2RS. Vein 2m-cu absent. Vein 1CU almost straight. Most part of the hind wings obscured. Legs not preserved due to incompleteness of the amber piece.

Metasoma completely preserved. Petiole elongate within *Cretevania* (see Table 1), 7.2 times longer than wide, slightly flattened laterally, with abundant short setae, 0.94 mm long, 0.13 mm at greatest width, with tergum and sternum fused, and with distal part expanded ventrally presenting a clear hump in the ventral surface (Figs 2, 3B). Gaster globe-shaped (spheroid), 1.26 mm long, 0.43 mm wide distally, and ca. 0.60 mm high distally, with abundant short setae (Fig. 2). A distal pair of short, ovoid, setose, exposed sclerites (appendages?) are present, which could correspond to male genitalia (absence of any structure resembling an ovipositor).

TABLE 1. Characters for diagnosing the currently described *Cretevania* species. Wing ratios measured from wing drawings shown in Peñalver *et al.* (2010), redrawn from the original publications. The total length of *C. alonsoi* has been more accurately estimated here (3.65 mm in the original publication).

CHARACTERS / *Cretevania* spp.	*alcalai*	*alonsoi*	*concordia*	*cyrtocerca*	*exquisita*	*major*	*meridionalis*	*minor*	*minuta*	*montoyai*	*pristina*	*rubusensis*	*vesca*	*soplaensis* nov. sp.
Total length	2.62	~ 4	?	3.4	7.1	?	3–3.5	?	> 2	3.14	6	1.90–2.10	7.7	~ 3.00
Flagellum uniformly thickened (i.e., not broader distally)	Yes	Yes	?	Yes	No	Yes	?	?	?	Yes	No	Yes	?	No
Forewing length	1.50	2.28	3.0–3.2	1.58	3.2	?	2–2.5	1.7	> 1.1	1.60	3.3	1.38	5.7	?
Forewing maximum width	0.57	0.95	1.3	0.8	?	?	?	0.67	0.80	0.70	?	0.54	?	~ 0.66
Ratio pterostigmal length/maximum width	4.2	2.7	4.1	2.3	5	4.5	3.5	5.8	5.2	4	3.4	4	4.1	3
Ratio first submarginal cell length/maximum width	7.4	3.8	4.6	4.8	5.8	7	> 5.9	6.9	5.1	5.1	4.7	~ 5.33	4.5	3.9
Vein 2RS shape: (S) - Nearly straight; (C) - convex subbasally	S	S	S	S	S	S	S	S	C	C	S	S	S	S
Ratio first marginal cell length/ maximum width	~ 3	2.1	3.3	3.7	3.1	3.4	4.1	3.9	4.4	2.2	3	2.4	3.4	2
Ratio length 1CU (or 1CUb+CUa)/ length 1m-cu	1.4	1.4	> 1.5	1.3	1.7	?	> 1.7	1.1	?	2.2	?	1.2	1.7	1
1r-rs shape: (S) - straight; (C) - concave	S	S	S	S	S	S	S	S	S	C	S	S	S	S
Vein 1r-rs arising near the pterostigma apex. (I) - intermediate	Yes	Yes	Yes	Yes	I	Yes	No	Yes	Yes	Yes	I	Yes	Yes	Yes
Vein rs-m: (N) - not evident; (T) - tubular; (S) - spectral	N	N	N	N	N	N	N	T	N	N	N	N	S	S
Track of rs-m or vestigial stub of rs-m nearly continuous with 1r-rs	Yes	Yes	No	No	No	Yes	?	No	Yes	No	No	Yes	Yes	Yes
Vein 2M shape: (S) - Nearly straight; (C) - concave subbasally	S	C	S	S	S	?	S	S	S	S	S	S	S	S
2CU+3CU with a steep change in its slope distally	Yes	Yes	Yes	No	?	?	Yes	Yes	?	Yes	Yes	Yes	?	Yes
2cu-a angled towards wing base	Yes	No	?	Yes	No	?	?	Yes	?	No	?	No	?	Yes
Wing apex shape: (R) - rounded; (P) - pointed	R	P	R	R	?	?	?	R	P	R	?	R	?	R
Ratio petiole length/maximum width	5.8	6.4	?	5.6	3.6	~ 5.5	?	6.2	5.6	5.8	4.8	~ 6.5	3.8	7.2

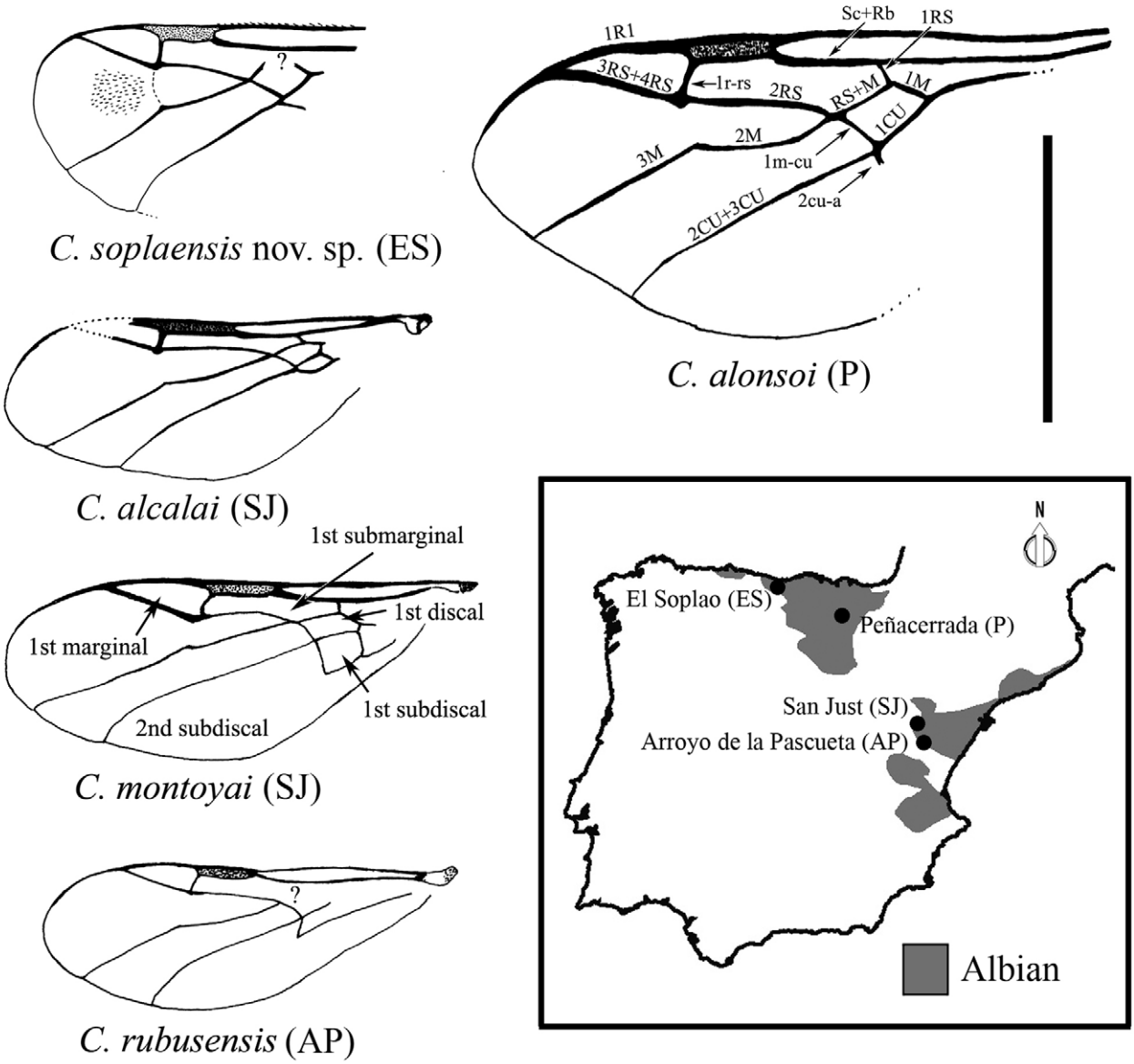

FIGURE 1. Camera lucida drawings of the forewings of the Spanish *Cretevania* species, including that of *C. soplaensis* nov. sp., holotype CES 364.2, from El Soplao amber, and geographical occurrences of the genus in the Spanish Albian. Basal portion of the forewing of *C. soplaensis* obscured. Previously described forewings from Peñalver *et al.* (2010). Scale bar = 1 mm. All the wings are to the same scale.

Discussion

We consider that the specimen is a male due to the absence of a thin, long, curved and exserted ovipositor characteristics of the genus; in addition, the gaster is globe-shaped, a morphology not observed in *Cretevania* female specimens but present in the holotype of *C. montoyai*, a supposed male (Peñalver *et al.* 2010).

The forewing vein pattern in the family Evaniidae is highly heterogeneous between genera and thus it is an important taxonomic character system. Forewing is only partially visible in the specimen, but it is distinct from other *Cretevania* species. The distal part of a hind wing is visible in a latero-ventral view of the specimen using reflected light, but significant features have not been observed. The body size and whole characters of forewings and antennae of the new species include it within the group constituted by the smallest Spanish species, found in amber outcrops from the Teruel Province (Fig. 1): *C. montoyai* and *C. alcalai* from San Just amber, and *C. rubusensis* from Arroyo de la Pascueta amber. Similarities are greater with respect to *C. alcalai*, but the latter differs from the new species in having a relatively longer pterostigma (4.4 times longer than wide), and a longer

and narrower first submarginal cell (7.4 times longer than wide); in addition, in *C. alcalai* the flagellum is uniformly thickened. Despite the holotype of *C. alcalai* has an incomplete gaster, it is similar in shape to that of the new species, but smaller and not as wide distally. *Cretevania rubusensis* can be distinguished from the new species in having a vein 2cu-a not angled towards wing base and antennae slightly squared in section, with the flagellum uniformly thickened. *Cretevania montoyai* differs from the new species in having a relatively longer pterostigma (4 times longer than wide), vein 2RS convex subbasally, 1CU (i.e., 1CUb+1CUa) 2.2 times longer than 1m-cu, vein 1r-rs concave, vestigial stub of rs-m more distally placed with respect to the vein 1r-rs, and vein 2cu-a not angled towards wing base. In contrast, both species share a similar metasoma in size and shape.

Cretevania alonsoi from Peñacerrada I amber mainly differs from *C. soplaensis* nov. sp by its greater size, in having a pedicel nearly half the length of flagellomere I, and a flagellum uniformly thickened. Although their vein patterns are strongly similar, *C. alonsoi* has the vein 2M concave basally, 2cu-a is not angled towards wing base, and the wing apex is pointed. Furthermore, the new species' forewing also displays a high resemblance to that of *C. cyrtocerca* from Lebanese amber, but the latter differs in a somewhat shorter pterostigma (ca. 2.3 times as long as wide), a longer first marginal cell (3.7 times longer than wide), and 2CU+3CU straight, i.e., lacking a steep change in its slope distally.

The forewing vein rs-m of *C. soplaensis* nov. sp. is spectral (Fig. 3F), as occurs in *C. vesca*, but this character is difficult to see and it is possibly also present in other species. On the contrary, the rs-m vein is tubular in *C. minor* (according to Rasnitsyn 1975, fig. 92a), a species also unique in having a tubular cross-vein 2m-cu in forewing.

The six Spanish specimens found represent five species. However, they have been found in four different amber outcrops, the dating of which has been not satisfactorily concluded. Hence, the fact that they could represent different episodes during the Albian could partially explain the observed diversity. The San Just outcrop has been dated as Middle Albian (Villanueva-Amadoz *et al.* 2010), while the rest apparently is Early Albian (Peñalver & Delclòs 2010). A study in progress is working towards the accurate dating of these and other Spanish amber deposits based on a more precise stratigraphical control and the study of the palynomorphs and dinoflagellate assemblages (Barrón, pers. comm.)

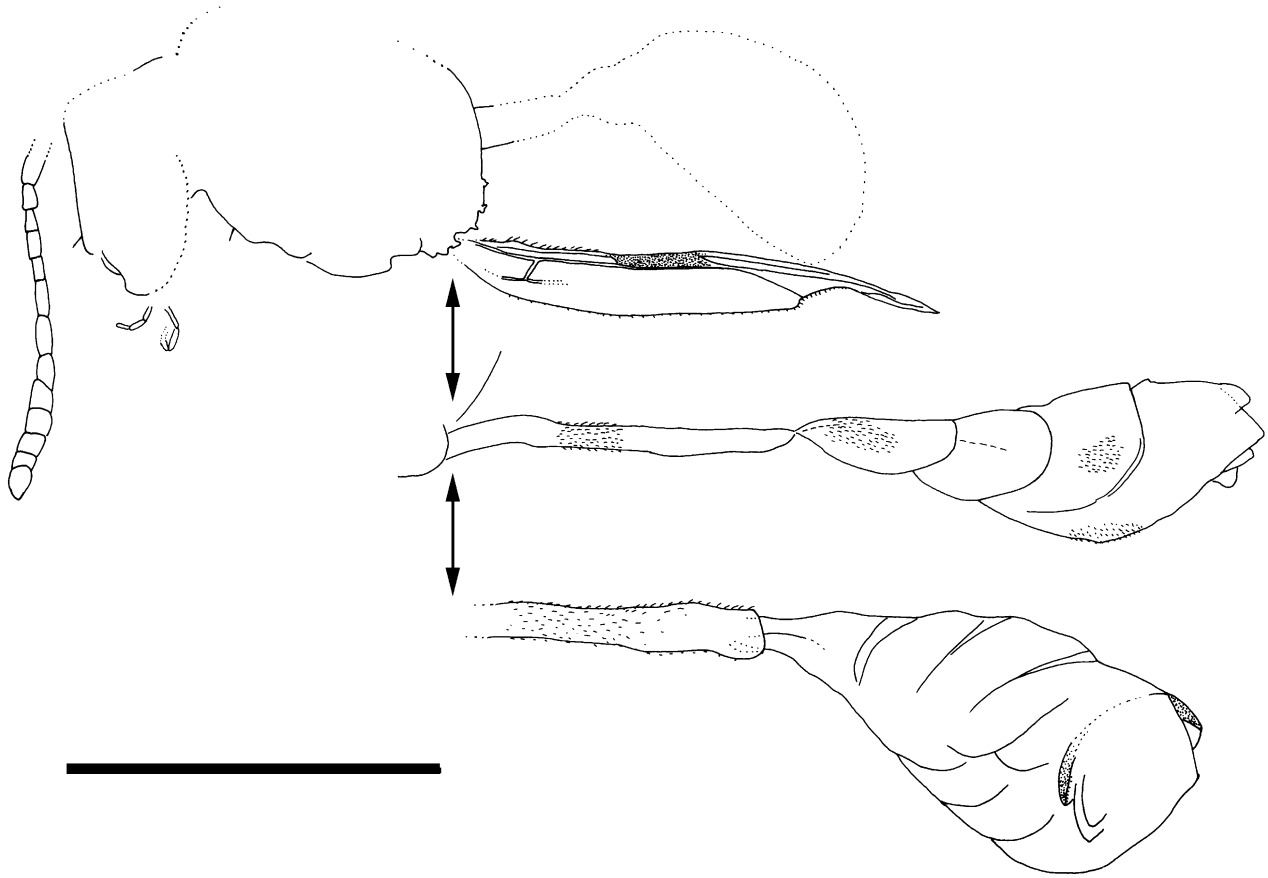

FIGURE 2. Camera lucida drawings of *Cretevania soplaensis* nov. sp., holotype CES 364.2, from El Soplao amber. Habitus in antero-lateral view showing the only preserved antenna and the metasoma, plus the metasoma in dorsal and latero-ventral views showing the distal hump in the ventral surface of the petiole. Scale bar = 1 mm.

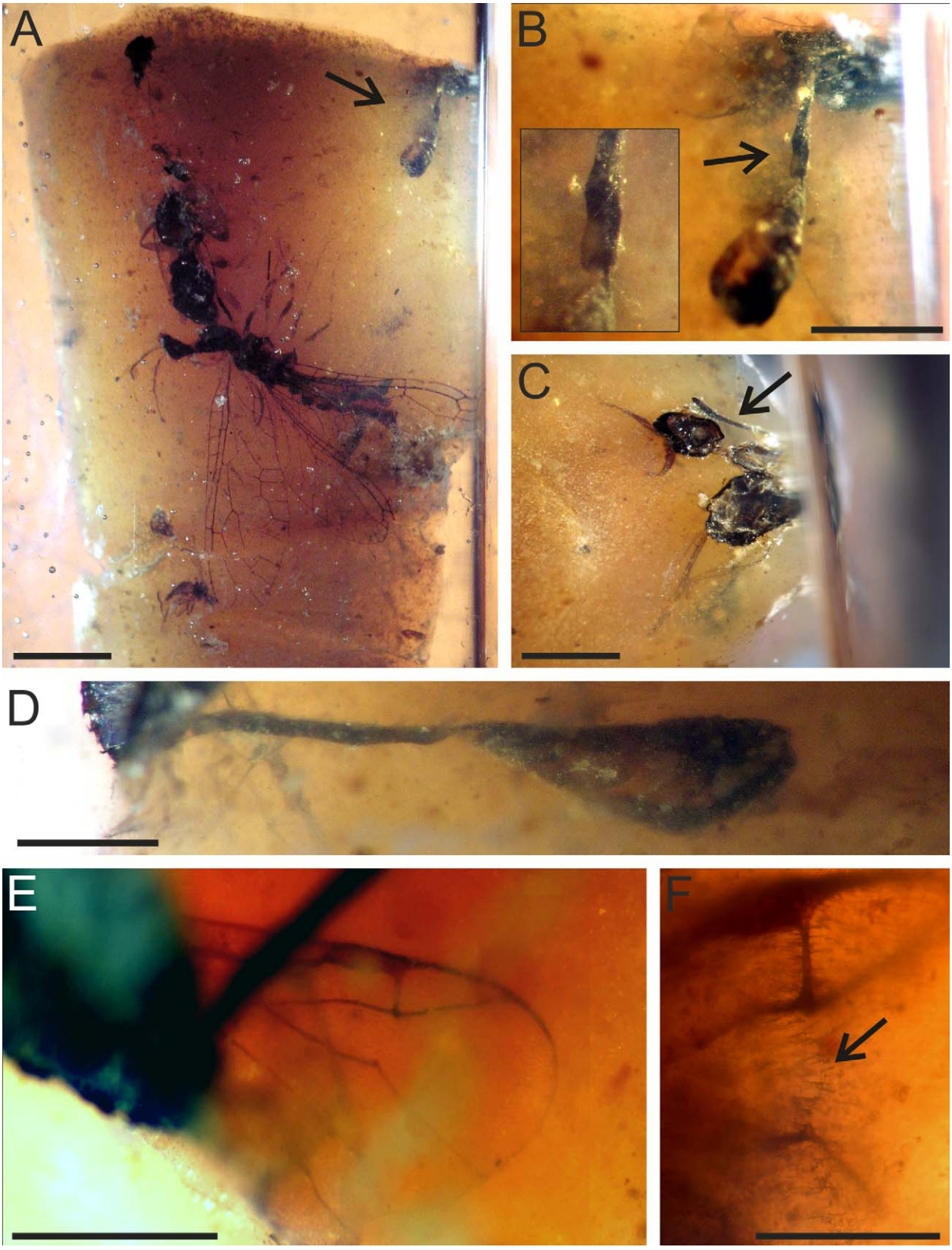

FIGURE 3. Photomicrographs of *Cretevania soplaensis* nov. sp., holotype CES 364.2, from El Soplao amber. A, amber piece containing the holotype (arrow) and other syninclusions as the mesoraphidiid *Alavaraphidia ventolina* Pérez-de la Fuente *et al*., 2012; B, detail of the holotype in latero-ventral view (inset showing enlargement of the distal hump in the ventral surface of the petiole); C, holotype in antero-lateral view showing the complete left antenna (arrow); D, petiole and gaster in dorsal view; E, visible portion of forewing (this image was made with two consecutive pictures taken at different focal planes); F, detail of the forewing showing the spectral vein rs-m (arrow). Scale bars: A = 2 mm, B, C = 1 mm, D, E = 0.5 mm, F = 0.2 mm.

Some of these Spanish specimens could represent the two sexes of the same species showing sexual dimorphism. Extant species of Evaniidae are often sexually dimorphic in coloration, setation, antennomere length and thickness, size of the compound eyes, and body sculpture (Deans & Huben 2003; Deans 2005; Kawada & Azevedo 2007). For example, female *Alobevania* has antennomeres progressively enlarging towards the apex (all antennomeres have the same diameter in male) and an exerted ovipositor (genitalia concealed in male) (Deans & Kawada 2008). Apparently, extant evaniids lack intraspecific sexual differences in body size and venation pattern. Regarding the Spanish fossils, the holotype of the new species could be a male of *C. alonsoi* based on the similar vein pattern of the visible areas of the forewing. However, this kind of relationship remains conjectural based on the current fossil evidence due to the following three reasons. First, the Spanish record is relatively scarce. Second, only four of the six Spanish specimens preserve the entire gaster, allowing reliable sex determination. The specimens described from non-Spanish localities are mainly incomplete or have important characters obscured, especially those preserved as compression fossils. For instance, the holotype of *C. concordia* from the Upper Hauterivian limestones of England is based on an isolated forewing. And third, no specimens were found as syninclusions in the same amber piece. It is extremely rare to find insects in copulation in Cretaceous ambers, but the presence of two morphotypes of the same genus and different sexes as syninclusions suggests sexual dimorphism. Unfortunately, the Spanish *Cretevania* specimens were not only found in different amber pieces but also in different amber deposits as indicated above. Increased collection and study of the Spanish amber could shed light about these observations.

In conclusion, the new described species further increases the Spanish diversity of the genus *Cretevania*, which, although scarce, is especially diverse in the Albian amber of Spain. Based on the biology of extant evaniids, as indicated by Peñalver *et al.* (2010), this fact could be related with the abundance of cockroaches in Spain during the Early Cretaceous.

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Anexo I.9

New Orchestina *Simon, 1882 (Araneae: Oonopidae) from Cretaceous ambers of Spain and France: first spiders described using phase-contrast X-ray synchrotron microtomography*

Nuevas *Orchestina* Simon, 1882 (Araneae: Oonopidae) de los ámbares cretácicos de España y Francia: primeras arañas descritas usando microtomografía por contraste de fase con radiación X sincrotrón

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Resumen:

Se describen dos nuevas especies del género *Orchestina* (Araneae: Oonopidae), *O*. *gappi* sp. nov. y *O*. *rabagensis* sp. nov., de los ámbares cretácicos de Francia y España, respectivamente. Dos especímenes españoles adicionales se clasifican en el género *Orchestina* pero sin asignación específica. Estas descripciones formales son las más antiguas para el género y la familia Oonopidae. El descubrimiento de estas ancestrales *Orchestina* no es sorprendente, en tanto en cuanto el género se considera un miembro basal de Oonopidae y uno de los más diversos y longevos linajes de arañas. Dos de las arañas se estudiaron en la European Synchrotron Radiation Facility mediante microtomografía por contraste de fase con radiación X sincrotrón, demostrándose una vez más el gran potencial de esta técnica para el estudio de inclusiones en ámbar.

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NEW *ORCHESTINA* SIMON, 1882 (ARANEAE: OONOPIDAE) FROM CRETACEOUS AMBERS OF SPAIN AND FRANCE: FIRST SPIDERS DESCRIBED USING PHASE-CONTRAST X-RAY SYNCHROTRON MICROTOMOGRAPHY

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Abstract: Two new species of *Orchestina* (Araneae: Oonopidae) are described as *O. gappi* sp. nov. and *O. rabagensis* sp. nov. from the Cretaceous of France and Spain, respectively. Two additional specimens from Spain are placed within *Orchestina* but not assigned to species. These formal descriptions are the oldest for the genus and the family Oonopidae. The discovery of these older *Orchestina* is not surprising, as the genus is considered a basal member of the Oonopidae and one of the most diverse and long-lived spider lineages. Two of the spiders were imaged at the European Synchrotron Radiation Facility using propagation phase-contrast X-ray synchrotron microtomography, demonstrating once again the enormous potential of this technique for studying fossil inclusions in amber.

Key words: Arachnida, goblin spiders, amber, Archingeay-Les Nouillers, El Soplao, San Just, Peñacerrada I.

OONOPIDAE Simon, 1890 are small, ecribellate, haplogyne spiders with six eyes and two claws on a pronounced onychium (Jocqué and Dippenaar-Schoeman 2006). The family is relatively diverse, with more than 684 extant species in 82 genera. Of the haplogyne families, only the Pholcidae encompasses more species (1122; Platnick 2011). Oonopids are free-living, nocturnal hunters and are distributed throughout the world, primarily in the tropics and subtropics. They live in a variety of habitats, such as under bark and stones, in leaf litter, among foliage and in the webs of other spiders (Saaristo 2001; PBI 2010).

Oonopids belong in the superfamily Dysderoidea, containing the Dysderidae Koch, 1837, Segestriidae Simon, 1893*a*, Oonopidae, and Orsolobidae Cooke, 1965 (Forster and Platnick 1985; Platnick *et al.* 1991). Within the Dysderoidea, the family is most closely related to the Orsolobidae based on the shared presence of tarsal proprioreceptor bristles and bipectinate tarsal claws (Forster and Platnick 1985; Platnick *et al.* 1991).

The oonopid fossil record is fairly extensive, comprising over three per cent of described fossil spider species (Dunlop *et al.* 2011). Oonopids have been found in more amber deposits than any other spider family (Penney 2007; Dunlop *et al.* 2011), although they are absent from the sedimentary rock record (probably as a result of their small size, see Martínez-Delclòs *et al.* 2004; Selden and Penney 2010; Penney and Selden 2011). The oldest oonopid was reported from Lebanese amber (late Barremian–early Aptian; Penney 2000) but, hitherto, Cretaceous oonopids have only been described from Burmese (late Albian; Penney 2000, 2006*a*; Rasnitsyn and Ross 2000; Grimaldi *et al.* 2002; Wunderlich 2008), New Jersey (Turonian; Penney 2002*a*, *b*; 2004) and Canadian (Campanian; Penney 2006*a*) ambers. Wunderlich (2008, p. 57) mentioned Cretaceous Chinese representatives of the Orchestininae, but the reference was to Fu Shun amber, which is Tertiary in age. Almost all described Cretaceous fossil diversity can be attributed to the genus *Orchestina*

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Simon, 1882, which is one of the oldest known lineages among extant spiders (Wunderlich 2004*a*).

The genus *Orchestina* dates back to the Cretaceous and represents the most common and diverse oonopid lineage in the fossil record, with 28 formally described fossil species (Dunlop *et al.* 2011). According to Wunderlich (2008), 10 per cent of Baltic amber spiders may be undescribed *Orchestina* specimens. The first fossil *Orchestina* was described from Baltic amber by Menge (1854) as *Segestria pusilla* (Wunderlich 1981, 2004*a*). The lineage is undoubtedly monophyletic (Saaristo 2001; PBI 2010) and is diagnosed primarily on the enlarged fourth femur used for jumping (Saaristo 2001; Marusik and Wunderlich 2008; PBI 2010).

Here, we describe four new specimens of the genus *Orchestina* (two new species) based on amber material from the Cretaceous of France and Spain. The specimens were discovered in amber from the (1) Font-de-Benon quarry near the village of Archingeay, Charente-Maritime, France (Perrichot and Néraudeau 2009), and from northern and eastern Spain in the outcrops of (2) Peñacerrada I (= Moraza, Burgos Province; Alonso *et al.* 2000), (3) San Just (Teruel Province; Peñalver *et al.* 2007) and (4) El Soplao (Cantabria Province; Najarro *et al.* 2009). These descriptions add to our knowledge of the diversity of the lineage at a relatively early point in its history.

Two of the *Orchestina* specimens (IGR.ARC-28.2 and CPT-4100) were imaged at the European Synchrotron Radiation Facility (ESRF) on beamlines ID19 and BM5 using propagation phase-contrast X-ray synchrotron microtomography (PPC-SRμCT). Although this technique was originally designed for surveying the palaeobiological content of opaque French Cretaceous amber, the method also allows for nondestructive viewing of minute morphological details that are not visible by conventional methods in translucent samples (Tafforeau *et al.* 2006; Lak *et al.* 2008; Soriano *et al.* 2010). The technique generates three-dimensional reconstructions and can reveal internal structures, if preserved. Here, we detail the first spiders to be formally described using PPC-SRμCT. Microtomographic imaging of spider specimens has been previously applied, but all of these studies used conventional X-ray microtomographic machines (e.g. Dierick *et al.* 2007; Penney *et al.* 2007; Selden *et al.* 2008; Bosselaers *et al.* 2010; Penney *et al.* 2011).

AMBER LOCALITIES

The Archingeay-Les Nouillers locality (herein referred to as Archingeay) is the most fossiliferous Cretaceous French amber deposit (Perrichot *et al.* 2007). The specimen originates from the lowermost of two amber-bearing strata exposed in the Font-de-Benon quarry, i.e. the A1sl-A level *sensu* Batten *et al.* (2010) = A1sl1 *sensu* Néraudeau *et al.* (2002). The dating of A1sl-A remains problematic; it contains dinoflagellate cysts suggesting a latest Albian age (Néraudeau *et al.* 2002; Dejax and Masure 2005), while megaspores recently discovered are more indicative of the early Cenomanian (Batten *et al.* 2010). The deposit is unique in that a large percentage of the inclusions represent litter fauna (Néraudeau *et al.* 2002). Four arachnid orders have been found in Charentes amber, comprising nine per cent of the arthropod inclusions, including 38 individuals of Araneae (Perrichot *et al.* 2007; Perrichot *et al.* 2010). Only one spider has been formally described from the deposit (Saupe and Selden 2009), but others were referred to by Schlüter (1978) and Néraudeau *et al.* (2002), and members of the family Zodariidae were mentioned as being present by Perrichot (2004) and Perrichot *et al.* (2007).

In Spain, there are three Cretaceous basins containing Albian amber: the Central Asturian Depression and the Basque-Cantabrian Basin, which drained to the proto-Atlantic, and the Maestrat Basin, which drained to the Tethys (Delclòs *et al.* 2007; Peñalver and Delclòs 2010). The Maestrat Basin lies to the east with several outcrops, the better known of which is San Just near Utrillas village (Peñalver *et al.* 2007). Two other important outcrops occur in the north of Spain within the Basque-Cantabrian Basin: Peñacerrada I in the north-east (Alonso *et al.* 2000; Delclòs *et al.* 2007) and El Soplao in the north-west (Najarro *et al.* 2009, 2010). All localities are associated with continental to marine environments. The Basque-Cantabrian Basin experienced more marine influences than the Maestrat basin. Sedimentologically, the amber deposits of the Maestrat Basin are associated with fluvial swamps, whereas amber deposits of the Basque-Cantabrian Basin are associated with delta-shore marine environments (see synthesis in Peñalver and Delclòs 2010).

The amber from Álava (Peñacerrada I & II outcrops), Basque-Cantabrian Basin, is well documented, with more than 2300 arthropod inclusions discovered to date (Alonso *et al.* 2000; Peñalver and Delclòs 2010). Araneae make up 2.4 per cent of these inclusions (Delclòs *et al.* 2007). Pollen analysis suggests an early Albian age (Barrón *et al.* 2009; Peñalver and Delclòs 2010). Thus far, two spiders have been formally described: a lagonomegopid (Penney 2006*b*) and an araneid (Penney and Ortuño 2006), while others were figured in the study by Alonso *et al.* (2000) and mentioned in the study by Delclòs *et al.* (2007).

The El Soplao outcrop is early Albian in age and located in the north-western part of the Basque-Cantabrian Basin. The deposit is potentially the largest amber site with arthropod bioinclusions in Spain (Najarro *et al.* 2009, 2010), with more than 400 discovered to date. The tarsal claws and silk of a spider were figured in Najarro *et al.* (2009), but no description was made, making the one herein the first.

The San Just outcrop is middle Albian in age and located in the Maestrat Basin (Oliete sub-basin) in Teruel Province (Peñalver *et al.* 2007; Peñalver and Delclòs 2010). Over 200 inclusions have been discovered thus far. Herein, we formally describe the first spider from San Just, which was figured in Soriano *et al.* (2010). The only other spider-related bioinclusions mentioned from this outcrop include a spider web with trapped prey detailed in the study by Peñalver *et al.* (2006) and a spider figured in the study by Delclòs *et al.* (2007).

MATERIALS AND METHODS

All microtomographic data (original and segmented slices, scan parameters, segmentation files, pictures and animations) are available online in the open-access ESRF palaeontology database (http://paleo.esrf.eu). The 3D models in ABS plastic are deposited with the type material in their respective institutions.

IGR.ARC-28.2 and MCNA-12593 were cut and polished, and CES-013 and CPT-4100 were encased in epoxy resin, prior to being received by the authors. Drawings of CES-013 and MCNA-12593 were carried out under incident and transmitted light with the aid of a camera lucida attached to a Leica M205 C stereomicroscope. Drawings were then inked and scanned into Adobe Photoshop CS4. Photographs of CES-013 and MCNA-12593 were taken using a Canon EOS 5D Mk II camera attached to Leica M205 C and Leica DM2500 M microscopes. Image stacks were merged using Helicon Focus 4.2.1 software (HeliconSoft Ltd.). Measurements for CES-013 and MCNA-12593 were captured with an ocular graticule, and measurements for IGR.ARC-28.2 and CPT-4100 were obtained using the scale provided with the synchrotron imaging. All measurements are in mm.

PPC-SRμCT

IGR.ARC-28.2 and CPT-4100 were imaged at the ESRF in Grenoble, France. IGR.ARC-28.2 was scanned on the ID19 beamline, with a set energy of 20 keV, a propagation distance of 50 mm, voxel size of 0.7 μ and 2000 projections with 0.2 s of exposure time. CPT-4100 was scanned on the BM05 beamline, with a set energy of 20 keV, a propagation distance of 100 mm, voxel size of 1.4 μ and 1500 projections with 2 s of exposure time.

Abbreviations. Terminology used in this paper is after Saaristo and van Harten (2006), although we refer to the structure bearing the opening of the seminal duct as the embolus rather than the sembolus; there is currently little evidence suggesting this structure is not homologous with the seminal duct of higher entelegynes. The embolus is polymorphic within the genus and can be blunt, tapering or bifurcate (Marusik and Wunderlich 2008). The relative proportions of the palpal segments and the embolus shape are considered useful in distinguishing among species of *Orchestina* (Wunderlich 2004*a*).

The bulbus index (ratio of bulbus width to height, BI), embolus index (ratio of bulbus width to embolus length, PBI) and patella index (ratio of male palpal patella width to length, PI) are utilized; these indices are considered helpful in diagnosing and describing *Orchestina* species (Saaristo and van Harten 2006). We introduce two new indices: the embolus characterization index (ratio of length of embolus to width of embolus at base: EI; not to be confused with the PBI) and the tibial index (ratio of palpal tibia width to length), which also may be useful in characterizing male *Orchestina*.

Anatomical abbreviations. Leg formula (e.g. 1423) indicates the length of each leg relative to the other legs from longest to shortest (in the example, 1 is the longest, followed by leg 4). ALE, anterior lateral eyes; ALS, anterior lateral spinneret(s); cx, coxa; cy, cymbium; em, embolus; fe, femur; MS, median spinneret(s); mt, metatarsus; PLE, posterior lateral eyes; PLS, posterior lateral spinneret(s); PME, posterior median eyes; pt, patella; ti, tibia; tr, trochanter; ts, tarsus.

Institutional and collection abbreviations. AMNH, American Museum of Natural History, New York, USA; CES, Colección El Soplao, Cueva El Soplao, Celis, Cantabria, Spain; CPT, Colección Paleontológica de Teruel, Teruel, Spain; ESRF, European Synchrotron Radiation Facility, Grenoble-Cedex, France; GPIMUH, Geological-Palaeontological Institute, University of Hamburg, Hamburg, Germany; MCNA, Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain; MNHN, Muséum national d'Histoire naturelle, Paris, France; SMNG, Senckenberg Museum für Naturkunde Görlitz, Görlitz, Germany.

Other material examined

Orchestina breviembolus Wunderlich, 1981; ♂ (holotype) from Baltic amber, GPIMUH 2526; ♂ (paratype) from Baltic amber, GPIMUH 2518; ♂ (paratype) from Baltic amber, GPIMUH 2501.

Orchestina colombiensis Wunderlich, 2004*b*; ♂ (holotype) from Colombian copal, SMNG 07136286.

Orchestina forceps Wunderlich, 1981; ♂ (holotype) from Baltic amber, GPIMUH 2524.

Orchestina furca Wunderlich, 1981; ♂♀ (holotype and paratype, respectively) from Baltic amber, GPIMUH 2519+.

Orchestina parisiensis Penney, 2007; ♂ (holotype) from Le Quesnoy amber (Paris Basin, France), MNHN A30090 (=PA 759); ♂ (paratype) from Le Quesnoy amber, MNHN A32049 (=PA 1909 1⁄3).

Orchestina sp. described in Penney, 2006*a*; juvenile from Burmese amber, AMNH-Bu-706.

Repository. The four specimens described here are deposited in the following institutions: (1) Department of Geosciences at the University of Rennes 1, Rennes, France; (2) Museo de Ciencias Naturales de Álava (MCNA), Vitoria-Gasteiz, Álava, Spain; (3) Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain; and (4) Institutional Collection from the El Soplao outcrop in the Laboratory of the El Soplao Cave, Celis, Cantabria, Spain.

SYSTEMATIC PALAEONTOLOGY

Order ARANEAE Clerck, 1757
Suborder OPISTHOTHELAE Pocock, 1892
Infraorder ARANEOMORPHAE Smith, 1902

Family OONOPIDAE Simon, 1890

Remarks. The monophyly of the Oonopidae was traditionally regarded as uncertain, and only two derived characters, the loss of cheliceral teeth and the loss of the female palpal claw, separated oonopids from other dysderoids (Platnick and Brescovit 1995; Platnick *et al.* 1991). Recently, Burger and Michalik (2010) discovered an additional synapomorphy (males possess an unpaired or completely fused testis) that may support the monophyly of the family.

Genus ORCHESTINA Simon, 1882

Type species. Schoenobates pavesii Simon, 1873, by monotypy. Recent from Spain, southern France, Corsica and Algeria.

Range. Early Cretaceous (early Albian from Spanish amber) to Recent.

Diagnosis. Orchestina belongs within the molles (soft-bodied) subgroup of the Oonopidae; the other subgroup consists of species with strong sclerotization (loricatae; Simon 1893*a*). The division is likely not monophyletic (PBI 2010) but corresponds to the subfamilies Oonopinae Simon, 1890 and Gamasomorphinae Petrunkevitch, 1923, respectively (Saaristo 2001).

The primary character diagnosing the genus *Orchestina* is the enlarged fourth femur, providing the ability to jump (Saaristo 2001). Although undoubtedly monophyletic, some authors have claimed that the group is diagnosed too broadly and is in need of revision (e.g. Saaristo 2001; Wunderlich 2008).

When paired with an enlarged fourth femur, other characters diagnostic for the genus are abdomen high and rounded, sclerotized seminal duct in the palpal bulbus, six eyes in segestriid position ('H' conformation) and the presence of a swollen palpal tibia, which is often wider and larger than the palpal femur (however, one fossil and two extant species do not share this trait; Marusik and Wunderlich 2008). The subfamily Orchestininae, created by Chamberlin and Ivie (1942), has not held up to scrutiny.

Remarks. All studied specimens possess the diagnostic enlarged fourth femur, six eyes in the segestriid position, a raised carapace and a rounded, high opisthosoma, placing them firmly within the genus *Orchestina*.

Orchestina gappi sp. nov.
Figures 1–5

Derivation of name. The specific epithet is after I. Wesley Gapp, a student of palaeontology with a contagious passion for the history of life on Earth.

Material. Holotype and only known specimen IGR.ARC-28.2, male (Figs 1–5); deposited in the amber collection of the Department of Geosciences at the University of Rennes 1, Rennes, France.

Preservation. The specimen is preserved in a piece of dark brown, fairly opaque amber $12 \times 6 \times 3$ in size. Syninclusions included a Psocoptera, a Diptera in the Chironomidae and a Dermaptera in the Pygidicranidae (V. Perrichot, pers. comm. 2010; Perrichot *et al.* 2011), although the piece was subsequently divided into two fragments (numbers ARC-28.1 to ARC-28.2) for optimal study. Only the dorsal side of the spider is visible using conventional methods; thus, PPC-SRμCT was utilized at the ESRF. The specimen is extremely well preserved, with only the opisthosoma suffering from dorso-ventral compression.

Locality and age. Font-de-Benon quarry, 1 km east of Archingeay-Les Nouillers (Charente-Maritime, France); uppermost Albian–lowermost Cenomanian (amber level A1sl-A; Néraudeau *et al.* 2002; Dejax and Masure 2005; Batten *et al.* 2010).

Diagnosis. Orchestina gappi sp. nov. can be distinguished from all other species by the concave shape of the bi-pronged embolus, which flares outward medially, reaching greatest width, and subsequently tapers distally. The longer embolus prong occurs entally. Further diagnostic characters include an ovoid, symmetrical palpal bulb with an embolus that emerges medially and a palpal tibia that bulges proximally.

Description. Body 1.00 long, small in size *sensu* Saaristo (2001), with length of carapace <0.60. Carapace 0.56 long, 0.49 wide, 0.20 wide at ocular region, 0.27 high; circular in outline, elevated into a dome that peaks past midpoint; steeply sloping carapace sides (Fig. 1); 16 setae present dorsally, *c.* 0.07–0.08 long; fovea absent. Clypeus fairly vertical, not sloping outward, 0.08 high; height 1.39× longer than width of PME; no indentations or projections present. Six eyes in segestriid position; subequal in size; PME contiguous with ALE in a row, with PLE above and contig-

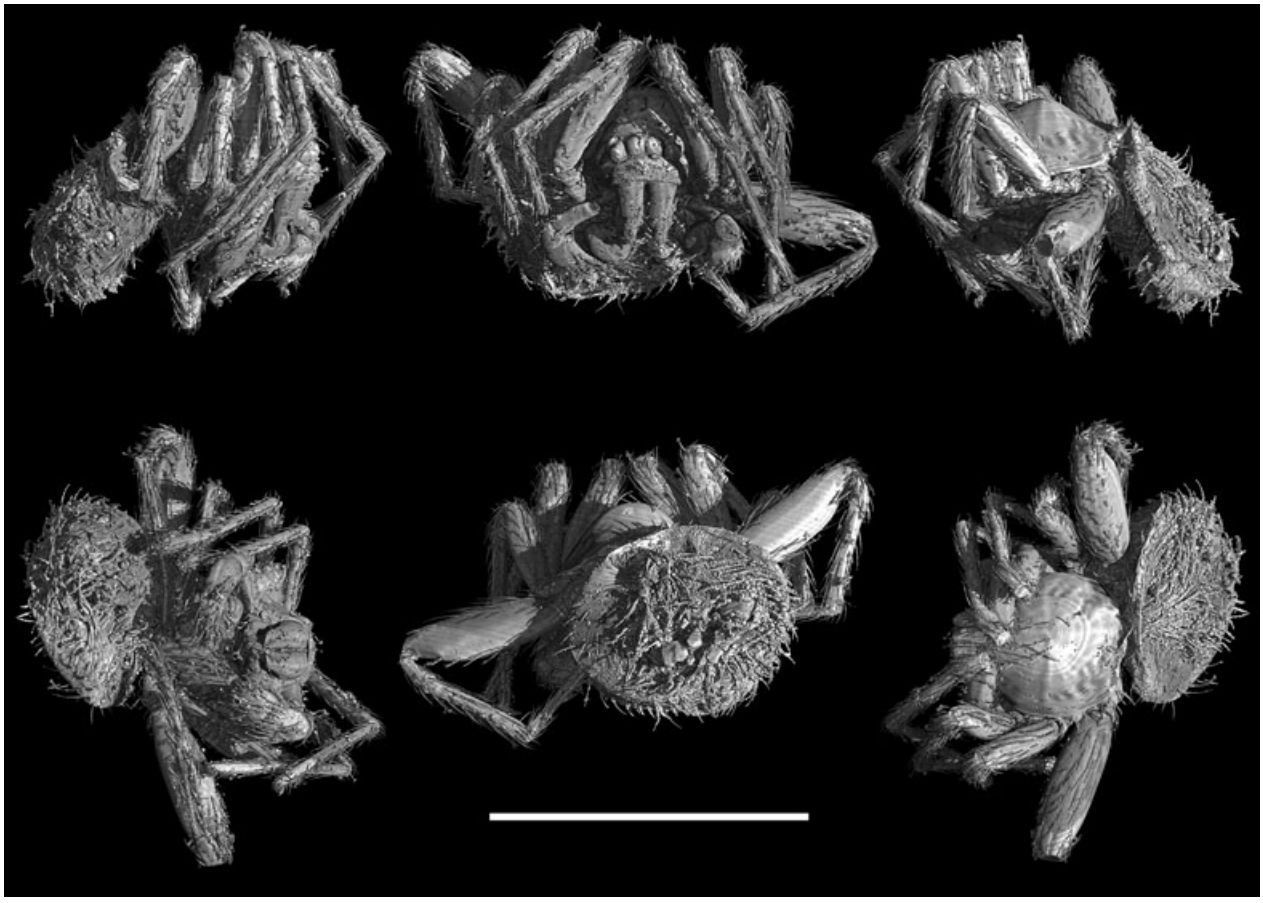

FIG. 1. 3D reconstruction of habitus of *Orchestina gappi* sp. nov., holotype IGR.ARC-28.2, ESRF, from the Font-de-Benon quarry, Archingeay-Les Nouillers (Charente-Maritime, France). Scale bar represents 1 mm.

uous with ALE; ALE wider than long and ovoid; PME longer than wide, ovoid; PLE kidney-shaped; one long seta projecting above each PLE. Chelicerae short, conical; 0.25 long, 0.10 wide at base; fang short. Labium kidney-shaped, wider than long, 0.10 wide at widest point. Endites cone-like and slender; *c.* 0.12 long, *c.* 0.05 wide; converging but not meeting. Sternum convex, heart-shaped with a blunt posterior end; *c.* 0.19 long, 0.32 wide at broadest point; no visible indentations near endites; approximately 14 setae present. Opisthosoma flattened dorso-ventrally, but probably ovoid to roundish in life; approximately 0.63 long, 0.70 wide; clothed in long setae about 0.09 long; no sclerites present. Six spinnerets positioned slightly ventro-anteriorly (Fig. 2); ALS and PLS divided into two, possibly three segments; ALS longer and wider than PLS, with MS smallest; right ALS 0.15 long, 0.06 wide; left ALS 0.12 long, 0.05 wide; right PLS 0.10 long, 0.03 wide; left PLS 0.09 long, 0.03 wide; right MS 0.07 long, 0.01 wide; left MS 0.09 long, 0.01 wide.

Leg formula 1423/4123; leg 1 cx 0.17, tr 0.07, fe 0.43, pt 0.16, ti 0.38, mt 0.40, ts 0.22, total 1.83; leg 2 cx 0.11, tr 0.06, fe 0.42, pt 0.16, ti 0.33, mt 0.40, ts 0.22, total 1.70; leg 3 cx 0.12, tr 0.06, fe 0.34, pt 0.14, ti 0.26, mt 0.30, ts 0.18, total 1.40; leg 4 cx 0.12, tr 0.06, fe 0.56, pt 0.18, ti 0.35, mt 0.35, ts 0.19, total 1.81. Leg 3 directed forward as in segestriids. Femur 4 enlarged; 1.3× longer than the average of the other femora and 1.58× broader than fe 3 (Fig. 1). Tarsal claws on distinct onychium; claws + onychium 0.05 long; claws with fine teeth. Legs clothed in simple setae, 0.06–0.09 long; apparently no spines present; serrate setae (if present) and trichobothria not visible because of the resolution used for synchrotron imaging.

Palpal segments; cx 0.05 long; tr 0.04 long; fe 0.14 long, 0.06 wide; pt 0.10 long, 0.09 wide; ti 0.17 long, 0.11 wide at broadest point; cy 0.13 long, 0.09 wide at broadest point. PI 0.89; TI 0.65; BI 0.62; PBI 0.83; EI 2.38. Femur fairly slender. Pt swollen. Ti swollen throughout, bulging proximally, covered with long setae, but not as dense as present on cy; trichobothria not visible because of the resolution used for synchrotron imaging. Cymbium triangular in shape with rounded corners, border visible; covered in elongated setae 0.07–0.10 long; cy fully covered by palpal bulb, with possible exception of most proximal part of cy; bulb inserted on ventral side of cy. Palpal bulb ovoid in shape, 0.16 high, 0.10 wide; width of bulb approximately equivalent to the width of ti at widest point (Figs 3–5). Embolus distinct from bulb, emerging almost medially from bulb in relation to where cy attaches; thick at base and throughout; 0.12 long, 0.05 wide at base, 0.06 wide at broadest point; structure concave half circle (i.e. curving upward); flaring out medially, particularly on ental side, in a quasi cup or diamond shape, and subsequently thinning; em bifurcated at tip, 0.03 wide at bifurcation, with two subcontiguous prongs; longer prong on ental side, 0.04 long; shorter prong 0.03 long (Figs 4–5).

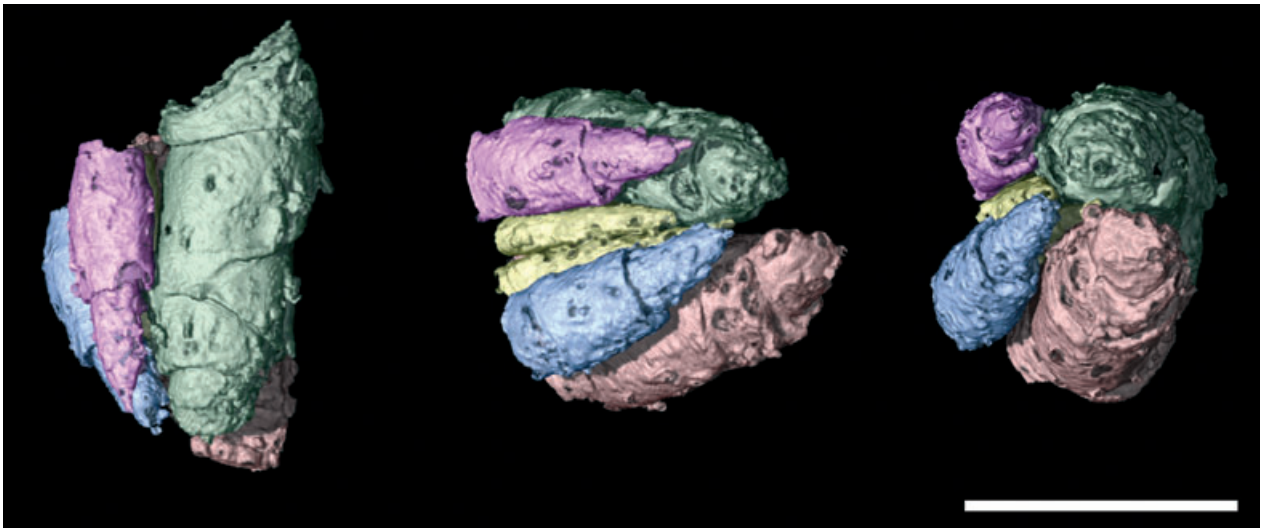

FIG. 2. 3D reconstruction of the spinnerets of *Orchestina gappi* sp. nov., holotype IGR.ARC-28.2, from the Font-de-Benon quarry, Archingeay-Les Nouillers (Charente-Maritime, France). Scale bar represents 100 μm.

Female. Unknown.

Remarks. No other species possess a bi-pronged, diamond-shaped embolus (i.e. flaring medially and curved upwards). Most *Orchestina* species have an embolus that is beak-shaped/convex (a notable exception is *O. parisiensis* from lowermost Eocene Le Quesnoy amber, but this species does not have an embolus that flares medially, and *O. manicata* Simon, 1893*b*, which possesses a pair of black apical dents on the embolus that are missing in *O. gappi* sp. nov.). Further, the palpal bulb of *O. gappi* sp. nov. is egg-shaped and symmetrical, with the embolus emerging medially. Other bulbs are lop-sided, triangular or otherwise shaped, with the embolus emerging from various positions. For example, *O. rabagensis* sp. nov. (this paper) has an embolus that emerges from the bulb distally. The tibial conformation of *O. gappi* sp. nov. is unique when in combination with the above characters: it bulges proximally and tapers distally, whereas other tibiae within *Orchestina* bulge throughout or distally.

Orchestina rabagensis sp. nov.
Figures 6, 7

Derivation of name. The specific epithet is after Rábago, the municipality in Cantabria (Spain) where the El Soplao outcrop is located.

Material. Holotype and only known specimen CES-013, male (Figs 6, 7); housed in the Institutional Collection from the El Soplao outcrop in the Laboratory of the El Soplao Cave, Celis, Cantabria (Spain).

Locality and age. El Soplao outcrop, Cantabria, Spain, early Albian (Najarro *et al.* 2009, 2010).

Preservation. The spider is preserved in a piece of clear, light yellow amber embedded in epoxy resin, $6 \times 6 \times 2$ in size. A platygastrid (parasitoid) wasp is present as a syninclusion. The specimen is complete with the exception of left legs I and II, which are cut at the tibiae. The cuticle is cleared in most of the specimen, with shrunken black remains within. The appendages are compressed, and the eyes and opisthosoma are shrivelled. The cuticle is pitted and particularly mesh-like on the palpal bulb. Barring this, the specimen is well preserved.

Diagnosis. Orchestina rabagensis sp. nov. can be distinguished from all other species by the combined presence of (1) a thin, relatively straight to slightly concave embolus with two long prongs widely separated from each other; (2) longer prong of the embolus positioned ectally; (3) embolus emerging from the bulb distally in relation to the cymbium; and (4) palpal tibia bulbus throughout.

Description. Body *c.* 1.10 long, small in size *sensu* Saaristo (2001), with the length of carapace <0.60. Carapace 0.56 long, *c.* 0.30 high, width not measurable; carapace probably oval in outline, moderately elevated into a dome that peaks at 2/3 of carapace length, resulting in the posterior carapace margin distinctly steeper than the anterior margin; steeply sloping carapace sides; *c.* 15 elongated setae present dorsally, 0.12 long; fovea absent (Fig. 6). Clypeus short, gently sloping forward, 0.04 long; indentations or projections not apparent. Six eyes, most likely in segestriid position, PME contiguous with ALE in a row, with PLE above and contiguous with ALE; eye morphology and measurements uncertain because of the preservation, though eyes similar in size; one long setae projecting above each PLE, 0.12

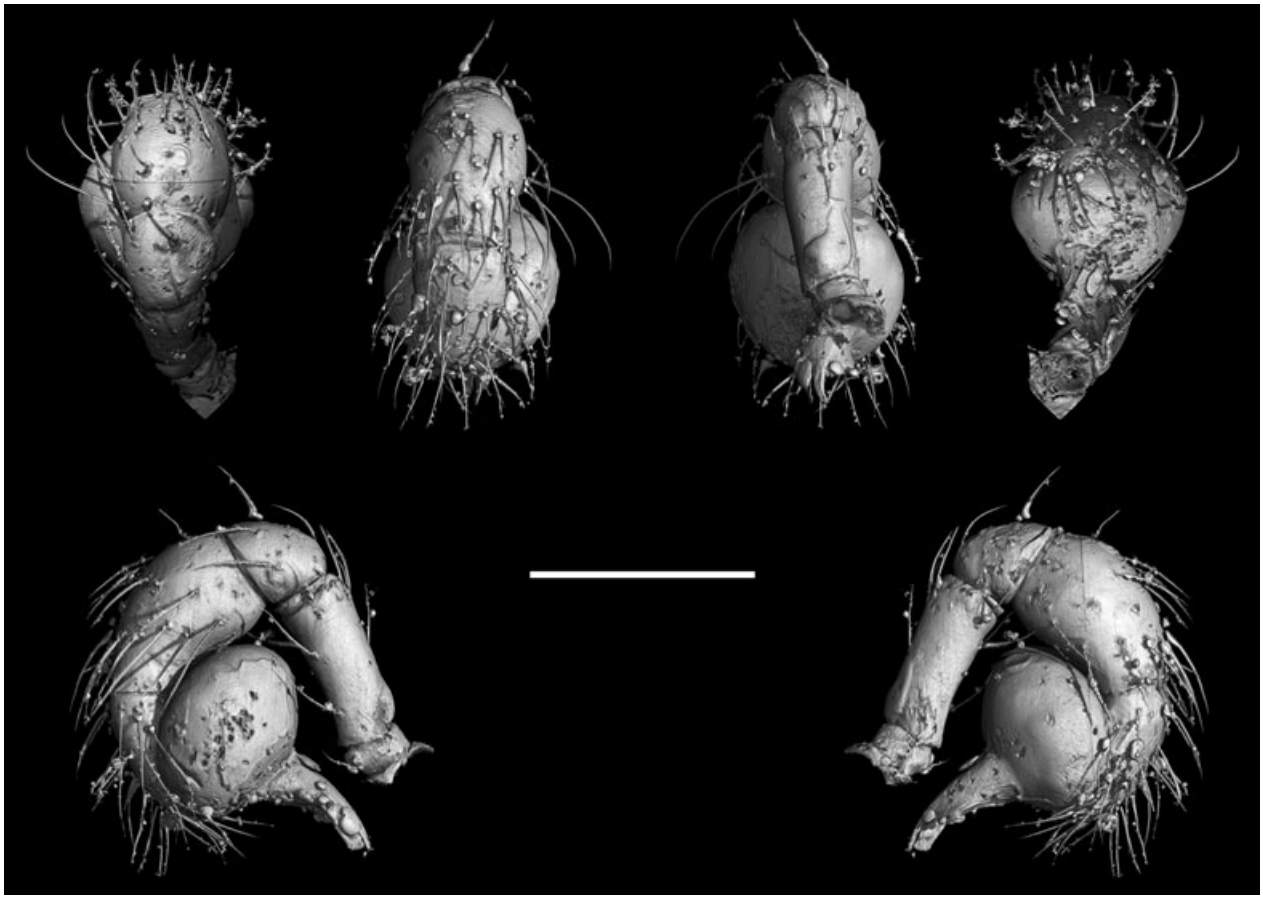

FIG. 3. 3D reconstruction of the left palpus of *Orchestina gappi* sp. nov., holotype IGR.ARC-28.2, from the Font-de-Benon quarry, Archingeay-Les Nouillers (Charente-Maritime, France). Lateral, ventral and dorsal views. Scale bar represents 200 μm.

long. Chelicerae short, tapering distally; 0.17 long, width not measurable; fang not visible. Labium, endites and sternum not visible. Opisthosoma morphology uncertain because of the preservation, but probably oval/drop-shaped; 0.52 long, 0.23 wide, 0.23 high as preserved; clothed in setae of about 0.07 length; apparently no sclerites present. Spinnerets not visible.

Leg formula 4213/2413; leg 1 cx 0.06, tr 0.05, fe 0.40, pt 0.15, ti 0.43, mt 0.33, ts 0.24, total 1.66; leg 2 fe 0.49, pt 0.15, ti 0.48, mt 0.36, ts 0.24, total 1.72 (cx and tr unknown); leg 3 fe 0.43, pt 0.12, ti 0.26, mt 0.31, ts 0.22, total 1.34 (cx and tr unknown); leg 4 cx 0.04, tr 0.04, fe 0.58, pt 0.15, ti 0.37, mt 0.45, ts 0.18, total 1.81. Possible space between cx 3 and 4. Femur 4 enlarged, 1.27× longer than the average of the other femora and approximately 1.3–1.4× broader than fe 3 (exact ratio not measurable as the other femora show compression). Tarsal claws on pronounced onychium; claws + onychium 0.06 long; claws with fine teeth. Legs clothed in setae 0.06–0.07 long; particularly elongated setae present in distal part of all fe, up to twice as long as other setae; serrate setae present on all mt and ts, serration more apparent on ts, also present on pt and ti of leg 4; short, rather thin spine on distalmost portion of fe 4. Trichobothria very elongated, up to 0.12–0.14 long, distinctly feathery (Fig. 7A), dorsally on ti and mt as follows: (1) one on 6/10 parts of ti 1 + 2; (2) two on ti 3, one on 1/5 parts and another on its midlength; (3) three on ti 4, close together along 3/5 of its length; and (4) one on almost distal tip of all mt. Tactile setae present, erect, short (0.03–0.04 long), not distinctly feathery, located dorsally and ventrally on ti, mt and ts (Fig. 7A), when occurring ventrally often arranged in pairs on mt and ts; longer tactile setae, 0.06–0.07 long, present dorsally on distal tip of ts 1 + 2.

Palpal segments; cx 0.04 long; tr 0.04 long, 0.04 wide; fe 0.11 long, 0.05 wide; pt 0.11 long, 0.05 wide at broadest point; ti 0.11 long, 0.08 wide; cy 0.08 long, 0.07 wide at broadest point. Palp laterally compressed so palpal indices may be misleading: PI 0.41; TI 0.73; BI 1.11; PBI 0.90; EI not determinable because width of em not measurable. Femur fairly slender. Patella appears elongate and thin. Tibia enlarged, bulbus throughout without tapering distally or proximally; covered with long setae but not as dense as in cy; one long trichobothria dorsally on midlength. Cymbium broad as preserved, triangular in shape with rounded corners, border visible; covered in elongated setae 0.09 long; cy fully covered by palpal bulb; bulb inserted on ventral side of cy. Palpal bulb likely ovoid in shape (shape distorted owing to lateral compression), 0.10 long, 0.09 wide; bulb cuticle particularly net-like. Embolus emerging more distally on bulb in relation to where cy attaches; thicker at base and tapering towards a bifurcating point (Fig. 7B); 0.11 long, 0.03 wide at base; em fairly straight, although curved slightly upward especially at tip (i.e. concave); em bifurcated slightly after

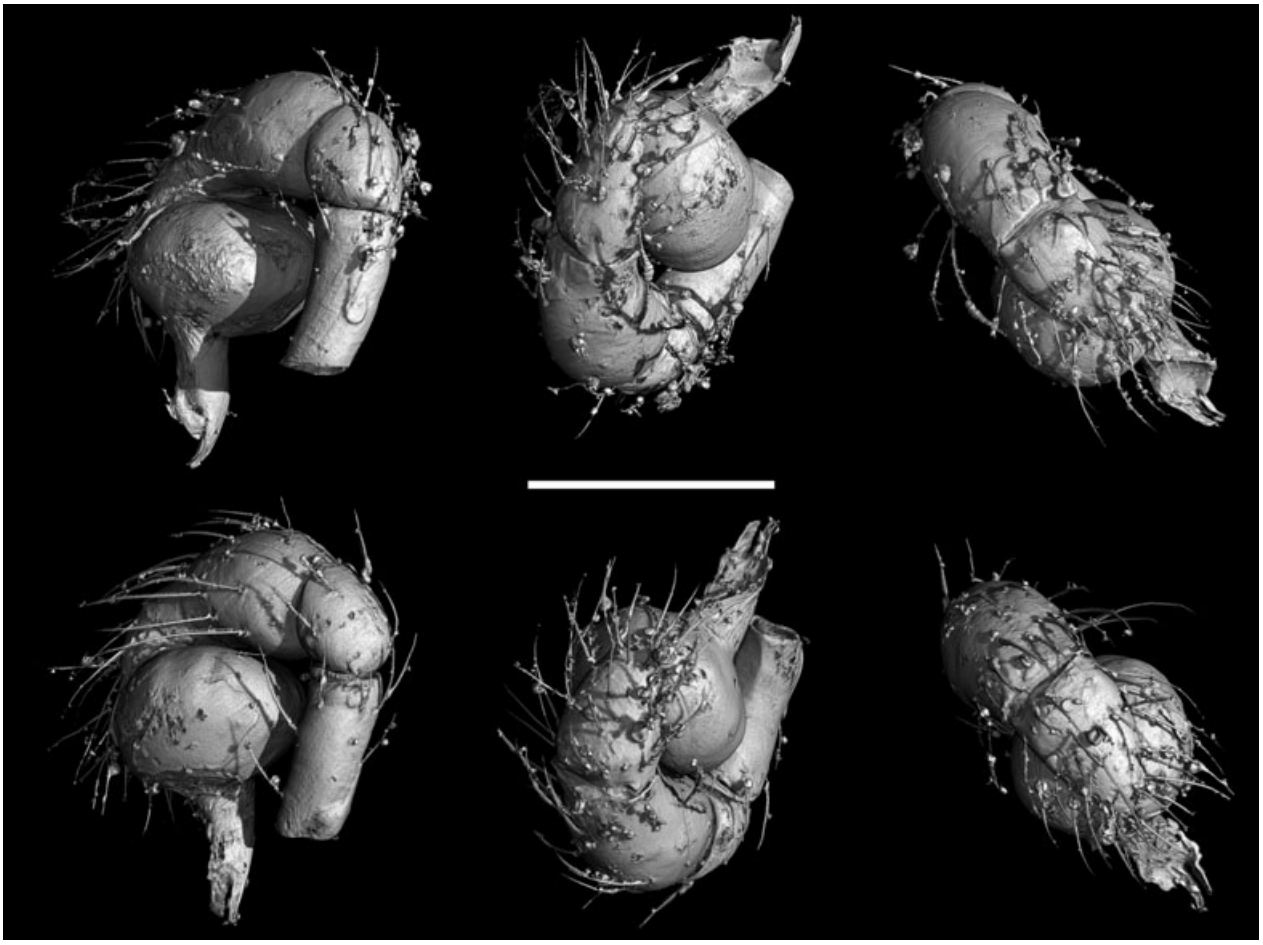

FIG. 4. 3D reconstruction of the left palpus of *Orchestina gappi* sp. nov., holotype IGR.ARC-28.2, from the Font-de-Benon quarry, Archingeay-Les Nouillers (Charente-Maritime, France). Oblique and dorsal views. Scale bar represents 200 μm.

its midpoint, 0.01 wide at bifurcation, with two prongs widely separated; longer prong on ectal/outer side, 0.05 long.

Female. Unknown.

Remarks. The widely separated prongs on a thin, tapering embolus are unique among *Orchestina*. Of the bi-pronged *Orchestina* species, none exhibit such a wide angle between the prongs and also possess such a dramatically tapering and relatively straight embolus (i.e. without kinks). *Orchestina colombiensis*, for example, has a long, thin embolus with two prongs, but the prongs are short and subequal in length. *Orchestina furca* possesses uneven prong lengths, but again, they are not widely spaced and the embolus is kinked (convex), not straight to slightly concave. A similar situation exists with *O. forceps*, while *O. longimana* Wunderlich, 1981 possesses widely spaced prongs, but the embolus is not tapering and emerges medially from the palpal bulb, not distally. It is interesting to note that the cymbium is much broader in *O. rabagensis* sp. nov. than in *O. gappi* sp. nov.

Orchestina sp. 1
Figures 8, 9

2010 *Orchestina* sp. Soriano *et al.*, fig. 4.1.

Material. CPT-4100, female deposited in the Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain.

Preservation. The specimen is preserved in a clear orange amber piece embedded in epoxy resin, 5 × 3 × 1.5 in size. Prosoma and opisthosoma are obliquely distorted, with the latter laterally crushed. The left and right legs are oriented in two subparallel planes. Abundant minute bubbles surround the opisthosomal setae and those leg segments in close contact. A coiled spider-web thread and a trichome are preserved as syninclusions.

Locality and age. San Just outcrop, Teruel, Spain, middle Albian (Delclòs *et al.* 2007; Peñalver *et al.* 2007; Peñalver and Delclòs 2010).

Description. Body 1.11 long, small in size *sensu* Saaristo (2001), with the length of carapace <0.60. Carapace 0.44 long, 0.35 wide,

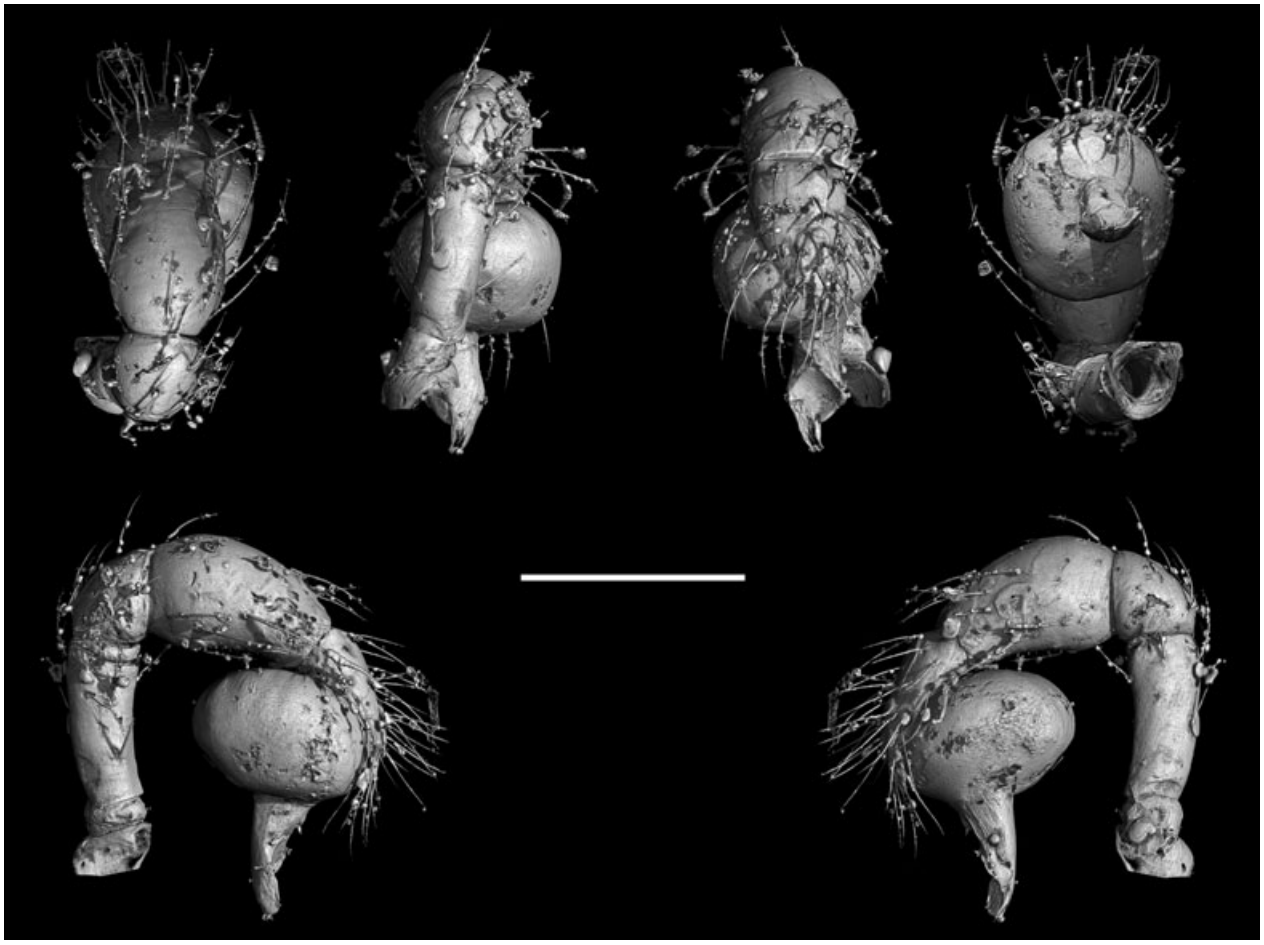

FIG. 5. 3D reconstruction of the right palpus of *Orchestina gappi* sp. nov., holotype IGR.ARC-28.2, from the Font-de-Benon quarry, Archingeay-Les Nouillers (Charente-Maritime, France). Lateral, ventral and dorsal views. Scale bar represents 200 μm.

0.17 wide at ocular region, 0.23 high; oval in outline, elevated into a dome that peaks at 2/3 of carapace length, resulting in the posterior carapace margin distinctly steeper than the anterior margin; steeply sloping carapace sides (Figs 8, 9); *c.* 20 elongated setae present dorsally, placed from behind the top of the carapace to above the eyes, 0.14 long. Clypeus fairly vertical, not sloping outwards, moderately short, 0.04 high; height 1.27× shorter than width of PME; no indentations or projections present. Six eyes in segestriid position; PME contiguous with ALE in a row, with PLE above and contiguous with ALE; PME eyes ovoid, 0.06 long, 0.06 wide; ALE almost circular, 0.06 long, 0.06 wide; PLE twisted so they appear more rhomboid shaped, 0.05 wide, 0.06 high. Chelicerae short, conical; 0.18 long, 0.08 wide at base; fang fairly short. Labium fan or delta-shaped, broader than long; 0.11 wide at widest point; with two subparallel lines dividing labium into three parts, central part slightly larger than laterals. Endites long and thin; 0.10 long, 0.04 wide; converging but not meeting. Sternum fairly convex, faintly heart-shaped but with a blunt distal end; 0.30 long, 0.30 wide at widest point; with slight projections between coxae; several setae present, 0.05–0.06 long. Opisthosoma bulbous and oval with an anterior-dorsal peak; 0.67 long (measured to tip of spinnerets), 0.38 wide at broadest point, 0.50 high at maximum height; clothed in long setae about 0.08–0.09 long; no sclerites present. Six spinnerets; ALS and PLS divided into at least two segments; ALS thickest and longest, 0.10 long, 0.04 wide; MS thinnest, 0.10 long, 0.01 wide; PLS 0.08 long, 0.03 wide.

Leg formula 4213/4123; leg 1 cx 0.10, tr 0.05, fe 0.36, pt 0.14, ti 0.28, mt 0.26, ts 0.22, total 1.41; leg 2 cx 0.10, tr 0.05, fe 0.36, pt 0.15, ti 0.28, mt 0.27, ts 0.21, total 1.42; leg 3 cx 0.10, tr 0.04, fe 0.31, pt 0.14, ti 0.22, mt 0.23, ts 0.19, total 1.23; leg 4 cx 0.12, tr 0.05, fe 0.40, pt 0.17, ti 0.27, mt 0.28, ts 0.19, total 1.48. Leg 3 projected forward as in segestriids with space between cx 3 and 4 (NB: only appears as such on left side). Femur 4 enlarged, 1.18× longer than the average of the other femora and 1.4× broader than fe 3. Tarsal claws on pronounced onychium; claws + onychium 0.06 long; claws with fine teeth. Legs clothed in setae 0.08–0.10 long, particularly elongated setae present on distal part of all fe, up to 0.14 long; serrate setae present on mt and ts, serration more apparent in ts; short, rather thin spine on distalmost portion of fe 4. Trichobothria elongated, about 0.10 long; distinctly feathery; dorsally on ti and mt as follows: (1) one on 6/10 parts of ti 1 + 2; (2) two on ti 3, close together along 3/5 of its length; (3) three on ti 4, close together along

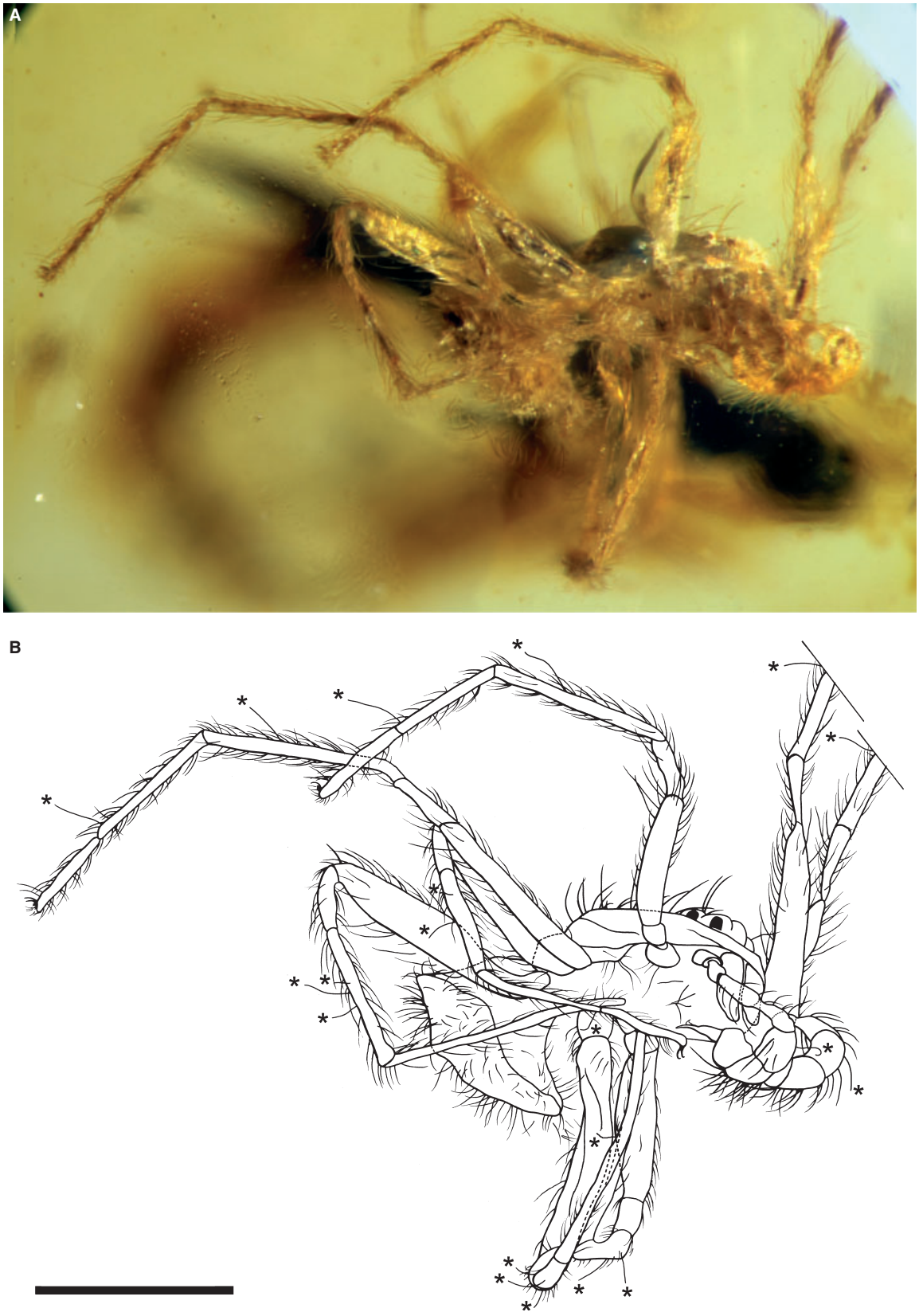

FIG. 6. *Orchestina rabagensis* sp. nov., holotype CES-013, from the El Soplao outcrop, Cantabria, Spain. A, lateral habitus. B, interpretive drawing, with stars representing noted trichobothria. Scale bar represents 0.5 mm for both images.

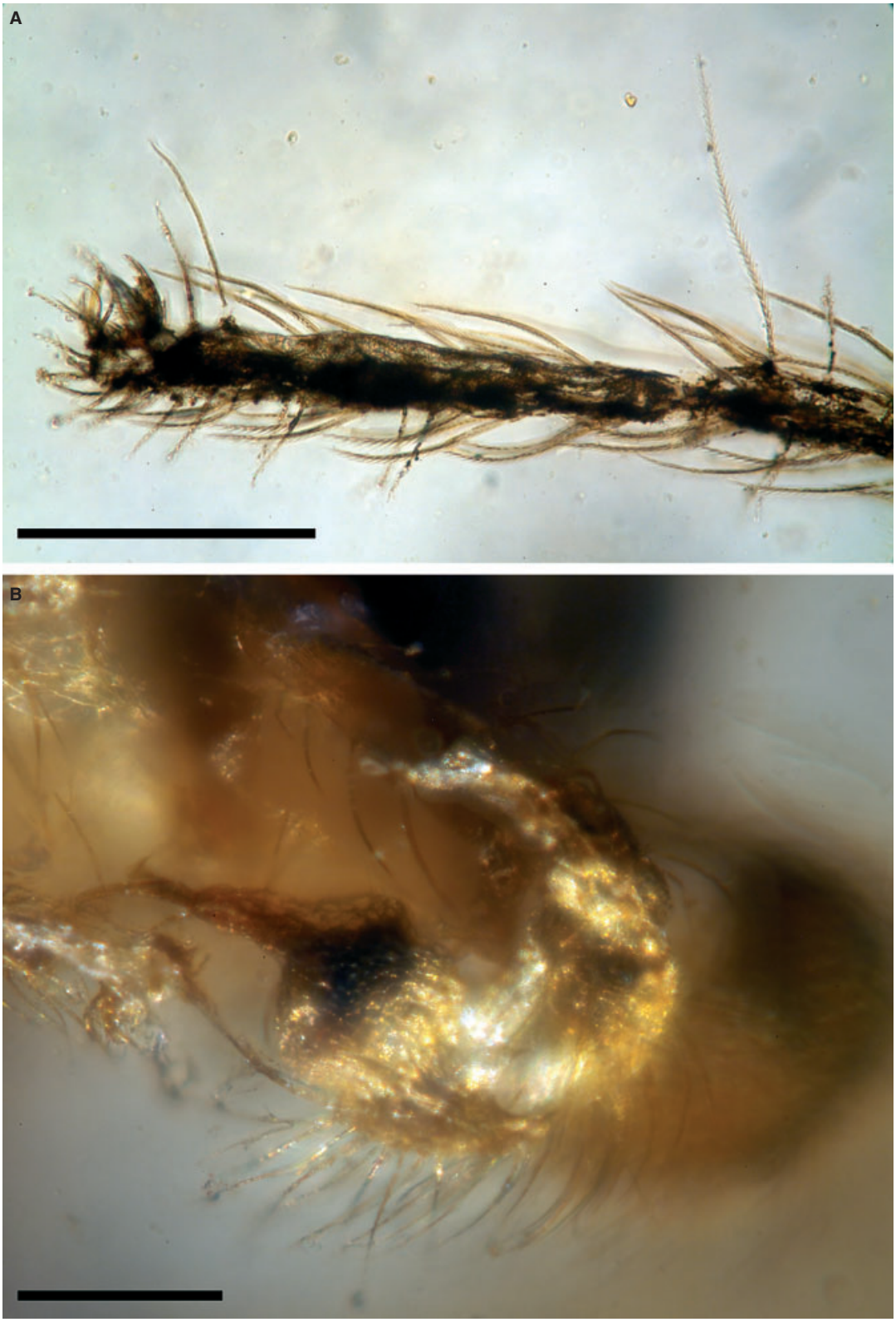

FIG. 7. *Orchestina rabagensis* sp. nov., holotype CES-013, from the El Soplao outcrop, Cantabria, Spain. A, tarsus and part of metatarsus. Note the elongated, feathery trichobothria on the distal portion of the mt, as well as the relatively short, erect, tactile setae on the ventral and dorsal ts and mt. B, lateral view of right palpus. Note the mesh-like appearance of the palpal bulb, likely a preservational artefact, and the long, divided embolus. Scale bars represent 0.1 mm.

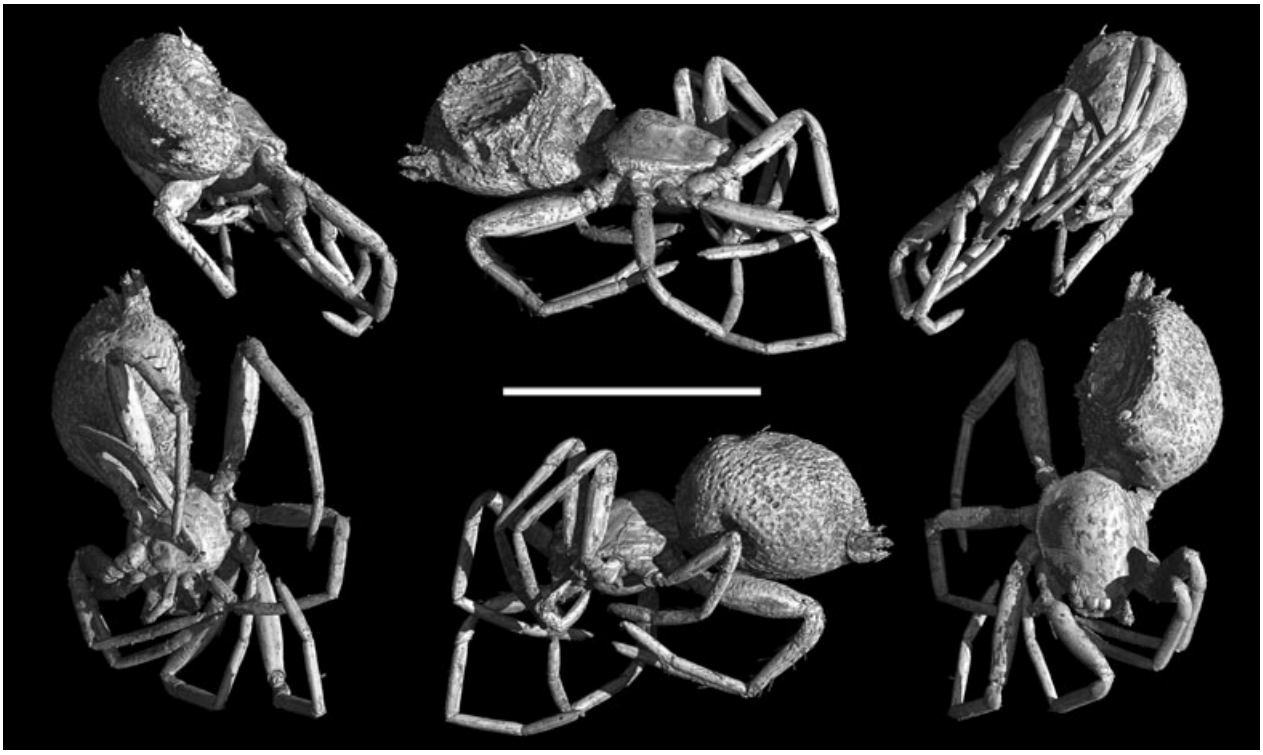

FIG. 8. 3D reconstruction of habitus of *Orchestina* sp. 1 (CPT-4100) from the San Just outcrop, Teruel, Spain. Scale bar represents 1 mm.

FIG. 9. Lateral habitus of *Orchestina* sp. 1 (CPT-4100) from the San Just outcrop, Teruel, Spain. Scale bar represents 0.5 mm.

3/5 of its length; and (4) one on almost distal tip of all mt. Some tactile setae present, erect, short (0.03 long), not distinctly feathery, located ventrally, a few on distal mt and a few pairs on ts of legs 1 + 2; longer tactile setae, 0.05 long, present dorsally on distal tip of all ti, mt and ts.

Palpus slender; cx 0.10 long; tr 0.02 long; fe 0.10 long; pt 0.08 long, 0.04 wide; ti 0.07 long, 0.04 wide; ts 0.16 long. Trichobothria not visible.

Orchestina sp. 2
Figure 10

Material. MCNA-12593, female; deposited in the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava, Spain.

Preservation. The specimen is embedded in a piece of clear, dark orange amber 12 × 6 × 1 in size. The amber is slightly clouded by organic debris. The spider is almost complete, with left leg 2 (possibly 1?) absent and the opisthosoma dorsally collapsed. The anterior left leg 1 (2?) is disarticulated and in connection with the anterior carapace. The legs exhibit different degrees of compression, although left femur 4 does not appear to be affected. A longitudinal amber fracture runs along the top of the carapace and one leg, whereas another crosses the ventral part of the opisthosoma. The specimen is preserved in fronto-dorsal view, and thus, the ventral characters of the prosoma are not currently visible. A thread of silk emerges from the right ALS.

Locality and age. Peñacerrada I (= Moraza) outcrop, Burgos, Spain, early Albian (Alonso *et al.* 2000; Delclòs *et al.* 2007; Peñalver and Delclòs 2010).

Description. Body length not measurable, but >1.00. Carapace length not measurable, 0.42 wide, 0.22 high at maximum height; ocular region width not measurable; carapace elevated into a dome that peaks at 2/3 of carapace length, resulting in the posterior carapace margin distinctly steeper than the anterior

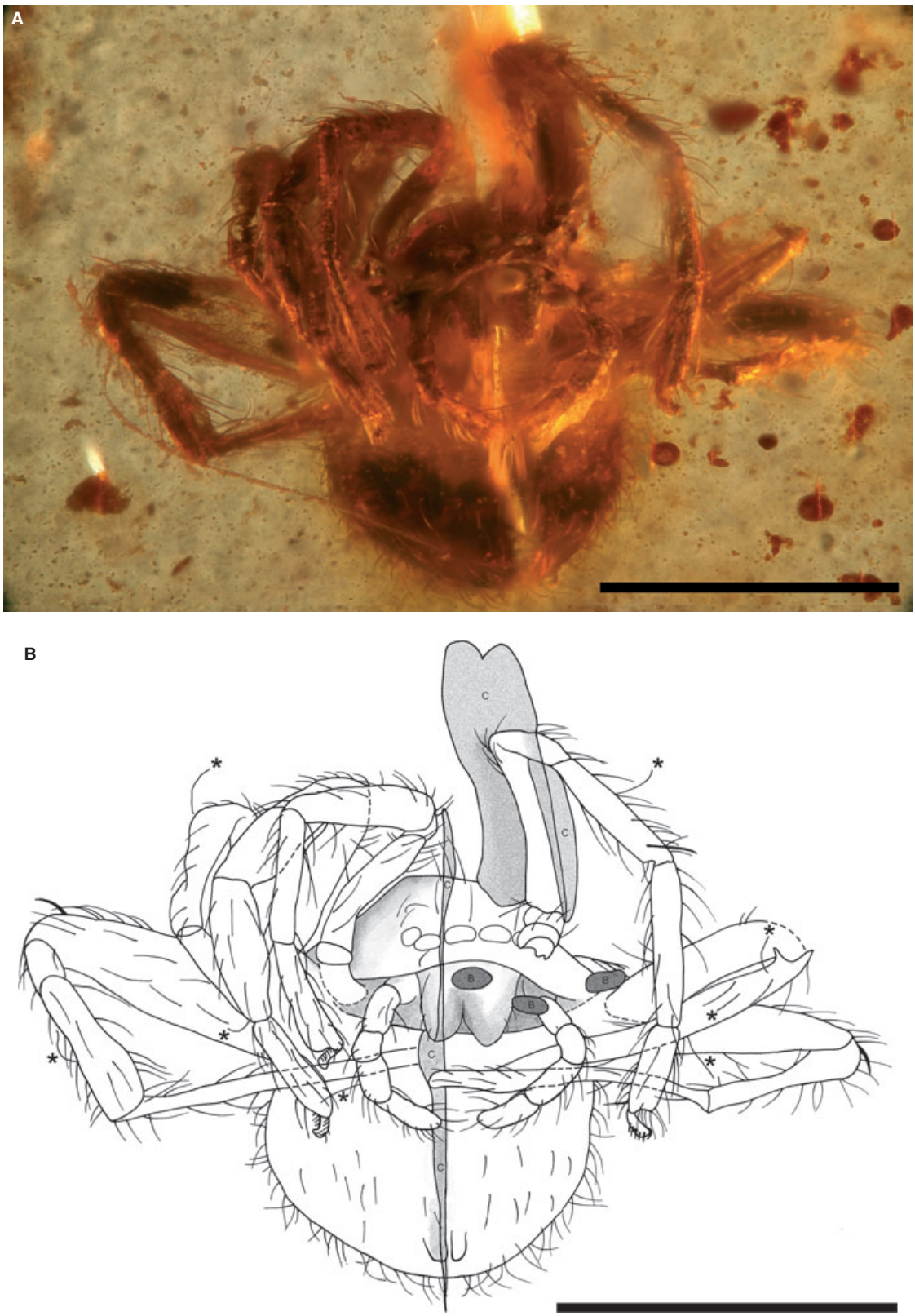

FIG. 10. *Orchestina* sp. 2 (MCNA-12593) from the Peñacerrada I outcrop (= Moraza), Burgos, Spain. A, frontal habitus. Note the silk thread emerging from the spinnerets to the left of the image. B, interpretive drawing with stars indicating known trichobothria. C = crack, B = bubble. Scale bars represent 0.5 mm.

margin; posterior margin probably concave (although crushed); steeply sloping carapace sides; at least eight setae present dorsally, 0.10 long; fovea not visible. Clypeus with a low slope, projecting outward, height not measurable; no indentations or projections present. Six eyes in segestriid position; PME contiguous with ALE in a row, with PLE above and contiguous with ALE; PME the largest, 0.05 wide, 0.03 high; ALE slightly smaller and more rounded than PME, 0.05 wide, 0.03 high; a few long setae present above ocular area. Chelicerae short, conical; 0.13 long, 0.05 wide at base; fang stout, length not measurable. Labium, endite and sternum not visible. Opisthosoma ovoid to rounded in shape; 0.50 long, 0.50 wide at maximum width; clothed in rather short setae of about 0.05 long; no sclerites present. Spinnerets positioned ventro-anteriorly; ALS longest and widest, length not measurable, 0.03 wide; PLS and MS difficult to discern.

Leg formula 4213; leg 1 cx 0.04, tr 0.02, fe 0.23, pt 0.05, ti 0.26, mt 0.21, ts 0.19, total 1.00; leg 2 fe 0.30, ti 0.25, mt 0.22, ts 0.19, total 0.96 (cx, tr and pt unknown, but if these lengths were considered, the total length would exceed leg 1 length); leg 3 fe 0.23, ti + mt + ts 0.50, total 0.73 (cx, tr and pt unknown); leg 4 fe 0.45, pt 0.08, ti 0.22, mt + ts 0.48, total 1.23 (cx and tr unknown). Femur 4 enlarged, 1.78× longer than the average of the other femora and approximately 1.5× broader than fe 3 (exact ratio not measurable as long as fe 3 shows compression). Tarsal claws on pronounced onychium; claws + onychium 0.05 long; claws with fine teeth. Legs clothed in setae 0.07–0.10 long; distinctly longer setae present on ventral side of ti 4, 0.08–0.09 long; serrate setae present on mt and ts, serration more apparent on ts; short, rather strong spine on distalmost portion of fe 4. Trichobothria very elongated, 0.12 long, distinctly feathery, dorsally on ti and mt as follows: (1) one on 6/10 parts of ti 1 (=ti 2?); (2) three on ti 3, one proximal, one medial and another distal; (3) one on midlength of ti 4; (4) one probably on distal mt 3; and (5) one on the distalmost tip of mt 1 (=mt 2?) and mt 3. A few tactile setae present, erect, short (0.04 long), not distinctly feathery, visible on distal ti 1 (=ti 2?) and at midlength of mt 1 (=mt 2?).

Palpus relatively stout; constant width throughout segments, 0.05 wide; fe 0.08 long, pt 0.05 long, ti 0.07 long, ts 0.12 long. One long trichobothria present dorsally at 4/10 parts of ti. Concentrated setae on distal end of palpal tarsus.

Remarks. We posit that CPT-4100 and MCNA-12593, both females and thus difficult to diagnose at species level, are not conspecific based on the following characters: the clypeus in CPT-4100 is vertical, whereas the clypeus in MCNA-12593 projects outward with a low slope. Other differences arise in setation; longer setae are present on the ventral side of ti 4 in MCNA-12593, while this trait is present on the ventral, distal ends of all femora in CPT-4100. MCNA-12593 possesses concentrated setae on the distal end of the palpal tarsus, but this character is absent in CPT-4100.

DISCUSSION

The exact relationships among species within the genus *Orchestina* have not been elucidated, and the group would benefit from phylogenetic analysis, particularly when combining extant and extinct diversity. Performing this sort of analysis at present, however, is not prudent when described species represent perhaps only 20 per cent of the true family diversity (PBI 2010). The Oonopid Planetary Biodiversity Inventory (PBI) is working towards more fully characterizing the family (PBI 2010), so this situation may soon change.

The two new species described herein seem to resemble those within the *O. pavesii* Group as designated by Marusik and Wunderlich (2008). According to these authors, this group includes the fossil species *O. forceps*, *O. furca* and possibly *O. colombiensis*; the extant species *O. pavesii*, *O. arabica* Dalmas 1916, *O. pavesiiformis* Saaristo, 2007, *O. manicata*, and four questionable species *O. bedu* Saaristo and van Harten, 2002, *O. mirabilis* Saaristo and van Harten, 2006, *O. hammamali* Saaristo and van Harten, 2006, and *O. lahj* Saaristo and van Harten, 2006. A bifid embolus tip seems to be the only diagnostic character supporting this assignment, which is potentially problematic as other species display this feature and were placed in different groups by Marusik and Wunderlich (2008).

Wunderlich (2008) erected two new genera for specimens described as *Orchestina* in Canadian and Burmese ambers. More specifically, he transferred the *Orchestina* species Penney (2006*a*) described from Cretaceous Canadian amber to *Canadaorchestina* Wunderlich, 2008. According to Wunderlich (2008), the undescribed Cretaceous New Jersey *Orchestina* mentioned by Penney (2002*b*, 2004) may also fall within *Canadaorchestina*. In the same volume, Wunderlich (2008) erected a new genus for those *Orchestina* found in Burmese amber, namely *Burmorchestina* Wunderlich, 2008; the Burmese specimen mentioned in Penney (2000) is considered a paratype of the monotypic species *B. pulcher* Wunderlich, 2008, but the undescribed *Orchestina* in Burmese amber of Penney (2006*a*) was not mentioned.

Neither *O. gappi* sp. nov. nor *O. rabagensis* sp. nov. place within Wunderlich's (2008) two new genera. Diagnostic characters for *Canadaorchestina* include slender palpal segments, a slender elongated bulbus and a long, thin, undivided embolus. As discussed, *O. gappi* sp. nov. and *O. rabagensis* sp. nov. have enlarged palpal segments, rounded bulbs and divided emboli. Similarly, diagnostic characters for *Canadaorchestina* include slender palpal articles and a large conductor on the palp, neither of which our specimens possess.

Whether Wunderlich's (2008) genera are valid is a matter of contention. While many have indicated the need for further division of the genus *Orchestina* (e.g. Saaristo 2001; Saaristo and Marusik 2004 with the creation of *Ferchestina*), the suggested diagnostic characters and rationale presented by Wunderlich (2008) are not especially convincing. The slender palpal articles are perhaps the

most striking character of both genera, but whether this warrants genus-level status is debatable. Further, because the Oonopid PBI will shed light on relationships within *Orchestina*, it might be best to refrain from subdivision until research within the group is further along. As it stands, the monotypic genera Wunderlich (2008) created are potentially paraphyletic and, if so, are not evolutionarily interesting.

CONCLUSIONS

The newly detailed palaeodiversity may significantly aid with the Oonopid PBI; first, because the specimens presented herein are among the oldest described oonopids, with the Spanish amber representatives being the oldest to date; and second, because according to the fossil record and as indicated by the eye pattern (PBI 2010), *Orchestina* may be the basalmost lineage of the family. The genus was already diverse and widespread by the Cretaceous, with recognized representatives in ambers from Spain (this paper), Myanmar (Penney 2006*a*), France (this paper), New Jersey (Penney 2002*b*, 2004) and potentially Canada (Penney 2006*a*).

In addition to providing information on the past biodiversity of this old group, we illustrate the utility of PPC-SRμCT imaging for studying minute details of specimens preserved in amber. The technique is particularly useful when analysing delicate characters with taxonomic importance (i.e. the male palps) and for unlocking details of specimens once partially or wholly obscured. The anatomical position of the spider itself often conceals vital characters such as the palp, sternum, labrum, endites and petiole, and thus, PPC-SRμCT is invaluable for revealing full character suites in these and similar situations.

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Anexo I.10

New lagonomegopid spiders (Araneae: †Lagonomegopidae) from Early Cretaceous Spanish amber

Nuevas arañas lagonomegópidas (Araneae: †Lagonomegopidae) del ámbar del Cretácico Inferior de España

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Resumen:

Se describen cuatro nuevas especies del ámbar del Albiense de España pertenecientes a la enigmática familia fósil Lagonomegopidae Eskov & Wunderlich, 1995. Se crean dos géneros: *Spinomegops* gen. nov., basado en dos especímenes descritos como *S. arcanus* sp. nov. del ámbar de Álava (yacimiento de Peñacerrada I, Burgos) y *S. aragonensis* sp. nov. del ámbar de San Just (Teruel), y *Soplaogonomegops* gen. nov., representado por la especie tipo *S. unzuei* sp. nov. del ámbar de El Soplao (Cantabria). Un único espécimen del ámbar de Álava se asigna tentativamente al género *Lagonomegops* Eskov & Wunderlich, 1995 y se describe como *L.*? *cor* sp. nov. Se confirma la existencia de numerosos tricobotrios tarsales y metatarsales en *Burlagonomegops alavensis* Penney, 2005, anteriormente discutida, y se reinterpreta la morfología de las piezas bucales de *Grandoculus chemahawinensis* Penney, 2004. A la luz de los nuevos datos, se enmienda la diagnosis de la familia Lagonomegopidae, y la familia Grandoculidae Penney, 2011 se sinonimiza con Lagonomegopidae.

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New lagonomegopid spiders (Araneae: †Lagonomegopidae) from Early Cretaceous Spanish amber

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Four new species belonging to the enigmatic fossil spider family Lagonomegopidae Eskov & Wunderlich, 1995 are described from Albian Spanish amber. Two new genera are created: *Spinomegops* gen. nov., based on two specimens described as *S. arcanus* sp. nov. from Álava amber (Peñacerrada I outcrop, Burgos) and *S. aragonensis* sp. nov. from San Just amber (Teruel); and *Soplaogonomegops* gen. nov., represented by the type species *S. unzuei* sp. nov. from El Soplao amber (Cantabria). A single specimen from Álava amber is tentatively assigned to *Lagonomegops* Eskov & Wunderlich, 1995 and described as *L.*? *cor* sp. nov. We confirm the existence of previously contentious numerous tarsal and metatarsal trichobothria on *Burlagonomegops alavensis* Penney, 2005, and reinterpret the mouthpart morphology of *Grandoculus chemahawinensis* Penney, 2004. In light of our new data, the family diagnosis for Lagonomegopidae is emended and Grandoculidae Penney, 2011 is synonymized with it.

Keywords: Arachnida; new taxa; Iberian Peninsula; Mesozoic; Albian

Introduction

The family Lagonomegopidae Eskov & Wunderlich, 1995 is a small group of spiders only known from inclusions in Cretaceous ambers. The family was placed within the superfamily Palpimanoidea primarily based on the presence of cheliceral peg teeth (Forster & Platnick 1984; Eskov & Wunderlich 1995). Lagonomegopids were named for the most diagnostic feature of the group: two large (*mega* in Greek) eyes (*-ops*) positioned on the anterolateral flanks (*lagono-*) of the carapace. This character is not found in any other fossil or extant spider family (Eskov & Wunderlich 1995; Jocqué & Dippenaar-Schoeman 2006). All fossils discovered to date (24 specimens) have been regarded as juveniles/females because of the absence of sexual differentiation in the male palp (note that Wunderlich 2008 reported a probable adult female but did not provide evidence for this assumption). While potentially unremarkable and reflecting the hand of chance or a taphonomic bias towards preservation of juvenile specimens in amber, because smaller organisms are more easily trapped in resin (Martínez-Delclòs *et al*. 2004), another explanation is that these spiders had a female-biased sex ratio, perhaps a consequence of parthenogenetic events. Female-biased sex ratios have been noted in some social (see Avilés 1997) and solitary (Gunnarsson & Andersson 1996) extant spiders, and Wunderlich (2004) reported an unusual sex ratio for members of the Baltic archaeid *Eoarchaea*, with more than 30 females and no males discovered. Although describing new taxa using putatively juvenile specimens can be problematic, the lagonomegopids described herein possess diagnosably distinct characters sufficient to delineate their diversity.

Four genera have been recognized within the family: *Lagonomegops* Eskov & Wunderlich, 1995, *Grandoculus* Penney, 2004, *Burlagonomegops* Penney, 2005, and *Zarqagonomegops* Kaddumi, 2007. *Lagonomegops* contains two species: *L. sukatchevae* Eskov & Wunderlich, 1995, based on two specimens from Coniacian–Santonian Taymir (Yantardakh) amber, and *L. americanus* Penney, 2005, from Turonian New Jersey amber (see description in Penney 2002). The genus *Grandoculus* consists only of the type species *G. chemahawinensis* Penney, 2004 from Campanian Cedar Lake amber, and was recently transferred to a new family by Penney (2011) (see below). Two species have been described within *Burlagonomegops*: *B. eskovi* Penney, 2005, from late Albian Burmese amber, and *B. alavensis* Penney, 2006 from Albian Álava amber. *Zarqagonomegops* Kaddumi, 2007 is represented by the type and only species: *Z. wunderlichi* from Albian Jordanian

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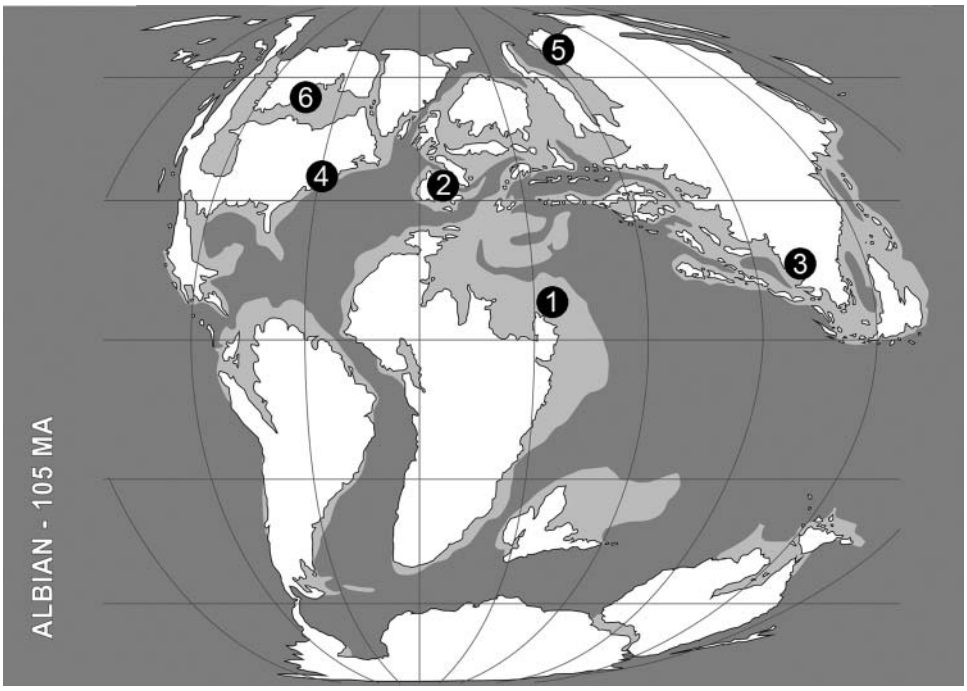

Figure 1. Cretaceous distribution of described Lagonomegopidae. The palaeogeographical map (redrawn from Blakey 2008) corresponds to the middle Albian (*c*.105 Ma). (1) Jordan (Albian): *Zarqagonomegops wunderlichi*. (2) Spain (Albian): (2.1) Álava amber, Peñacerrada I (= Moraza) and II outcrops (Burgos and Álava, respectively): *Burlagonomegops alavensis*, *Lagonomegops*? *cor* sp. nov., *Spinomegops arcanus* sp. nov.; (2.2) San Just amber (Teruel): *Spinomegops aragonensis* sp. nov.; (2.3) El Soplao amber (Cantabria): *Soplaogonomegops unzuei* gen. et sp. nov. (3) Myanmar (late Albian): *Burlagonomegops eskovi*. (4) New Jersey (Turonian): *Lagonomegops americanus*. (5) Yantardakh, Taimyr (Coniacian–Santonian): *Lagonomegops sukatchevae*. (6) Cedar Lake, Canada (Campanian): *Grandoculus chemahawinensis*.

amber. The diagnostic characters for *Zarqagonomegops* are weak, however, and Wunderlich (2008) suggested that the genus might be congeneric with *Lagonomegops*. More recently, 12 specimens regarded as *Burlagonomegops* ?*eskovi* were recognized from Burmese amber (Wunderlich 2008).

The widespread distribution of lagonomegopids during the Cretaceous (Fig. 1) and their absence from well-known Tertiary resins suggest that the family met its demise in the Late Cretaceous, perhaps related to the end-Cretaceous mass extinction event (Penney 2005). Based on the short legs and large eyes, lagonomegopids have been regarded as free hunters (not constructing a web) (Eskov & Wunderlich 1995), a condition present in most, if not all, palpimanoids (Forster & Platnick 1984). Others have hypothesized that, due to overall similarity in habitus, lagonomegopids occupied the same ecological niche as salticids (Eskov & Wunderlich 1995; Penney 2005), a diverse group of large-eyed, jumping spiders unknown from the Cretaceous (Dunlop *et al*. 2011), but this assertion remains conjectural at best.

Here we describe new lagonomegopids from Spanish Albian amber that significantly increase the diversity of the family and allow redefinition of its limits.

Geological setting

Two Cretaceous basins have yielded significant amber with bioinclusions in Spain: the Basque-Cantabrian Basin (northern Spain) and the Maestrat Basin (eastern Spain) (Delclòs *et al*. 2007). The amber deposits of the Maestrat Basin are associated with fluvial-swamp environments, while those of the Basque Cantabrian Basin are linked with deltaic-shore marine environments (see synthesis in Peñalver & Delclòs 2010).

The amber from the Peñacerrada I (= Moraza) outcrop belongs to the so-called Álava amber (Alonso *et al*. 2000), which is located in the eastern portion of the Basque Cantabrian Basin in Burgos Province. Three spiders have been described from Álava amber: the lagonomegopid *Burlagonomegops alavensis* Penney, 2006, an araneid, and an oonopid (Penney 2006; Penney & Ortuño 2006; Saupe *et al*. 2012). An additional spider was figured by Alonso *et al*. (2000, fig. 9.6). More than 2000 arthropod inclusions have been discovered from the outcrop, with Araneae comprising 2.4% of the diversity (Delclòs *et al*. 2007; Peñalver & Delclòs 2010).

The El Soplao outcrop is located in the north-western part of the Basque-Cantabrian Basin in Cantabria Autonomous

Community, near the locality of Rábago (Najarro *et al*. 2009). The deposit is potentially the largest amber site with bioinclusions in Spain (Najarro *et al*. 2010), and more than 400 arthropod inclusions have been obtained so far. Among spider fossils, only an oonopid has been formally described from this locality (Saupe *et al*. 2012), but the tarsal claws from an unidentified spider and spider silk were figured by Najarro *et al*. (2009, figs 9E, F).

The San Just outcrop is located in the Oliete sub-basin within the Maestrat Basin in Teruel Province (Peñalver *et al*. 2007). Over 200 bioinclusions have been discovered to date, including a recently described oonopid (Saupe *et al*. 2012), a spider web with trapped prey (Peñalver *et al*. 2006), and a figured spider (Delclòs *et al*. 2007, fig. 3F).

Geological and palynological studies indicate an Albian age for all these deposits (Alonso *et al*. 2000; Barrón *et al*. 2009; Najarro *et al*. 2009, 2010; Villanueva-Amadoz *et al*. 2010).

Material and methods

All amber pieces were cut, polished, and embedded in epoxy resin prior to receipt by the authors. Drawings of the specimens were made under incident and transmitted light with the aid of a camera lucida attached to a Leica DM2500 M microscope. Drawings were then inked and scanned into Adobe Photoshop CS4. Photographs were taken with a Canon EOS 5D Mark II camera attached to a Leica M205 C stereomicroscope and a Leica DM2500 M microscope. Image stacks were merged using Helicon Focus 4.2.1 software (HeliconSoft). All measurements were taken with an ocular graticule.

Eye homology follows Eskov & Wunderlich (1995). Leg formula (e.g. 1423) indicates the length of each leg relative to the other legs from longest to shortest (in the example, 1 is the longest, followed by leg 4). Larger fractions indicate more distally placed structures (e.g. a trichobothrium at one-third of tibial length is more proximal than one at two-thirds of tibial length). Trichobothria are marked with asterisks (*) in drawings and photographs.

Anatomical abbreviations

ALE: anterior lateral eye(s); ALS: anterior lateral spinneret(s); AME: anterior median eye(s); cx: coxa(e); fe: femur/-ora; MS: median spinneret(s); mt: metatarsus/-i; PLE: posterior lateral eye(s); PLS: posterior lateral spinneret(s); PME: posterior median eye(s); pt: patella(e); ti: tibia(e); tr: trochanter(s); ts: tarsus/-i.

Institutional abbreviations

CES: Colección El Soplao; **CPT**: Colección Paleontológica de Teruel; **MCNA**: Museo de Ciencias Naturales de Álava; **MCZ**: Museum of Comparative Zoology at Harvard University, Cambridge, MA, USA; **PIN**: Paleontological Institute of the Russian Academy of Sciences, Moscow.

Additionally examined samples

(1) *Burlagonomegops alavensis* Penney, 2006, holotype; Álava amber (Peñacerrada II outcrop), Álava, Spain. Deposited at the MCNA. Images of this sample were taken with a Leica DFC280 camera attached to a Leica M420 stereomicroscope and a Nikon Labophot2-Pol microscope. (2) *Grandoculus chemahawinensis* Penney, 2004, holotype; Cedar Lake amber, Manitoba, Canada. Deposited at the MCZ.

Trichobothria determination

The trichobothrial pattern in Lagonomegopidae has been granted taxonomic significance (cf. *Burlagonomegops*) but is often difficult to assess and has been embroiled in controversy. Accordingly, we point out the criteria employed for recognizing trichobothria in the studied lagonomegopids and for differentiating them from regular leg and tactile setae. Tactile setae are short, thin, erect hairs that act as sensory structures (mechanoreceptors) (Foelix 2011). They are usually found in lagonomegopids on distal podomeres, at least ventrally and dorsally. We acknowledge that some of the tactile setae recognized in the specimens described here could correspond to taste hairs (chemoreceptors) *sensu* Foelix (2011, fig. 4.15).

Four main criteria were followed, with three subsidiary guides depending on the circumstance: (1) trichobothria are thinner than regular leg setae and tactile setae; (2) trichobothria have a constant thickness, while regular leg setae and tactile setae taper towards their tip; (3) trichobothria, although variable in length, tend to be longer than regular leg setae and much longer than tactile setae; and (4) while trichobothria emerge from the dorsal part of the podomere, regular leg setae arise from all podomere positions; the same logic follows for tactile setae, which can be present ventrally. Subsidiary criteria are: (1) the bothrium (i.e. the often-ridged, dome-like organ from which the trich emerges) is sometimes conspicuous ~~(Fig. 8E)~~; however, tactile setae can arise from a relatively well-developed socket (Foelix 2011, fig. 4.1), and shrivelling can cause the base of regular leg setae to appear dome-like; (2) trichobothria are usually erect (i.e. emerge orthogonal to the leg podomere), whereas regular leg setae are adpressed to the podomere cuticle, and tactile setae are more obliquely disposed to the podomere surface; (3) trichobothria typically exhibit the flexible, sinuous structure present in life, while regular leg setae and tactile setae tend to be stiff; nevertheless, some tactile setae can be slightly sinuous ~~(Figs 4C, 6F)~~ and, depending on the biostratinomic processes (e.g. the spider's last movements in resin), trichobothria can appear stiff.

Even following these criteria, the determination of trichobothria is often a challenge and, in a few cases, it was difficult to ascertain whether a hair-like structure corresponds to a trichobothrium or a tactile seta ~~(Fig. 4B)~~. We note that the total absence of trichobothria reported from *Zarqagonomegops wunderlichi* is surprising and should be reassessed.

Systematic palaeontology

Order **Araneae** Clerck, 1757
Family **Lagonomegopidae** Eskov & Wunderlich, 1995

Type species. *Lagonomegops sukatchevae* Eskov & Wunderlich, 1995.

Emended diagnosis. Minute to small spiders (1 to nearly 5 mm). Cheliceral foramen absent. Chelicerae bearing several pointed, relatively short peg teeth (up to five) on the unguis. Carapace with two anterolateral protrusions, where a pair of large eyes (tentatively interpreted as the PME) are placed. Endites subtriangular, directed across the labium, almost meeting at the midline, with serrula as a single row of teeth. Labium subtriangular, wider than long. Sternum shield-like, without marginal projections between or at the middle of coxae. Six spinnerets. Several tibial trichobothria present, with the subdistal metatarsal trichobothria longest. Three tarsal claws, unpaired claw hook-like. Female palpal tarsi lacking a claw.

Remarks. Some characters show a wider variability within the current framework of Lagonomegopidae or have been impossible to assess from all species. Although they have not been included in the family diagnosis, other characters worthy of consideration are: carapace and chelicerae shape; number of eyes; presence of cuticular specializations on legs 1 + 2; presence of femoral spines; and further features associated with trichobothrial pattern. Among them, the number of eyes and the trichobothrial pattern are often difficult to discern in the specimens and can be easily overlooked in the descriptions.

Carapace shape ranges from compact to elongated, with varying degrees of elevation. The carapace can also have a distinct cephalic region, which can be projected forward, and the cephalic region, if distinct, can be constricted to different degrees, even forming a neck. Furthermore, the area of cheliceral insertion and mouthparts can be separated in the vertical plane (i.e. chelicerae can be inserted at an elevated point of the carapace).

Chelicerae range from almost straight to gently or strongly procurved, and their relative size (not only length) is variable.

Up to three additional pairs of smaller eyes may be present: up to two pairs (tentatively interpreted as the AME and ALE) below and slightly anterior to the large PME, and one pair (tentatively interpreted as the PLE) placed at the posterior margin of the anterolateral protrusions of the carapace.

Cuticular modifications on legs 1 + 2 can be present, composed of hairs forming scopulae (densely packed) or bristles hair- to spine-like in thickness and not forming scopulae (loosely arranged).

Erect, curved spines on distalmost femora, variable in thickness, are frequently present.

Apart from the trichobothrial characters delimited in the diagnosis, (1) the tibial trichobothria can be arranged in pairs; (2) additional, shorter metatarsal trichobothria can be present in a more proximal position; and (3) tarsal trichobothria can be present.

Genus ***Lagonomegops*** Eskov & Wunderlich, 1995

Type species. *Lagonomegops sukatchevae* Eskov & Wunderlich, 1995 (holotype PIN ~~PIM~~ 3311/564; paratype PIN ~~PIM~~ 3311/573; the current location of this material is unknown (Penney 2005; Rasnitsyn & Eskov pers. comm. 2012)).

Occurrence. Early to Late Cretaceous (Albian to Coniacian–Santonian). *Lagonomegops americanus* Penney, 2005, from Turonian New Jersey amber; *L. sukatchevae* Eskov & Wunderlich, 1995, from Coniacian–Santonian Yantardakh amber, Taimyr.

Lagonomegops*? *cor sp. nov.
(Figs 2, 3)

Diagnosis. Carapace almost as long as high (ratio prosomal length/height close to 1), with maximum height reached anteriorly; heart-shaped when viewed from above, resulting from greatest carapace width reached anteriorly and the conspicuous frontal protrusions that create a pronounced, acute frontal depression. Tarsi not longer than metatarsi.

Derivation of ~~the~~ name. The specific epithet is the Latin term *cor*, meaning heart, and is treated as a noun in apposition (hence in nominative case). The name refers to the heart-shaped outline (in abstraction) of the carapace when viewed from above.

Material. MCNA-13295, juvenile or adult female from Álava amber, Peñacerrada I (= Moraza) outcrop (Burgos, Spain). The cuticle is clear, especially in the proximal part of all legs, almost to the point of invisibility. Remains of cuticle cut diagonally through the prosoma. The opisthosoma is lifted above the prosoma, with the distal portion not preserved. Most of leg 2 is missing. A bubble occurs inside the left PME, and several others are present inside some leg segments. The specimen is preserved together with a fragmentary long leg of an undetermined arthropod and organic debris.

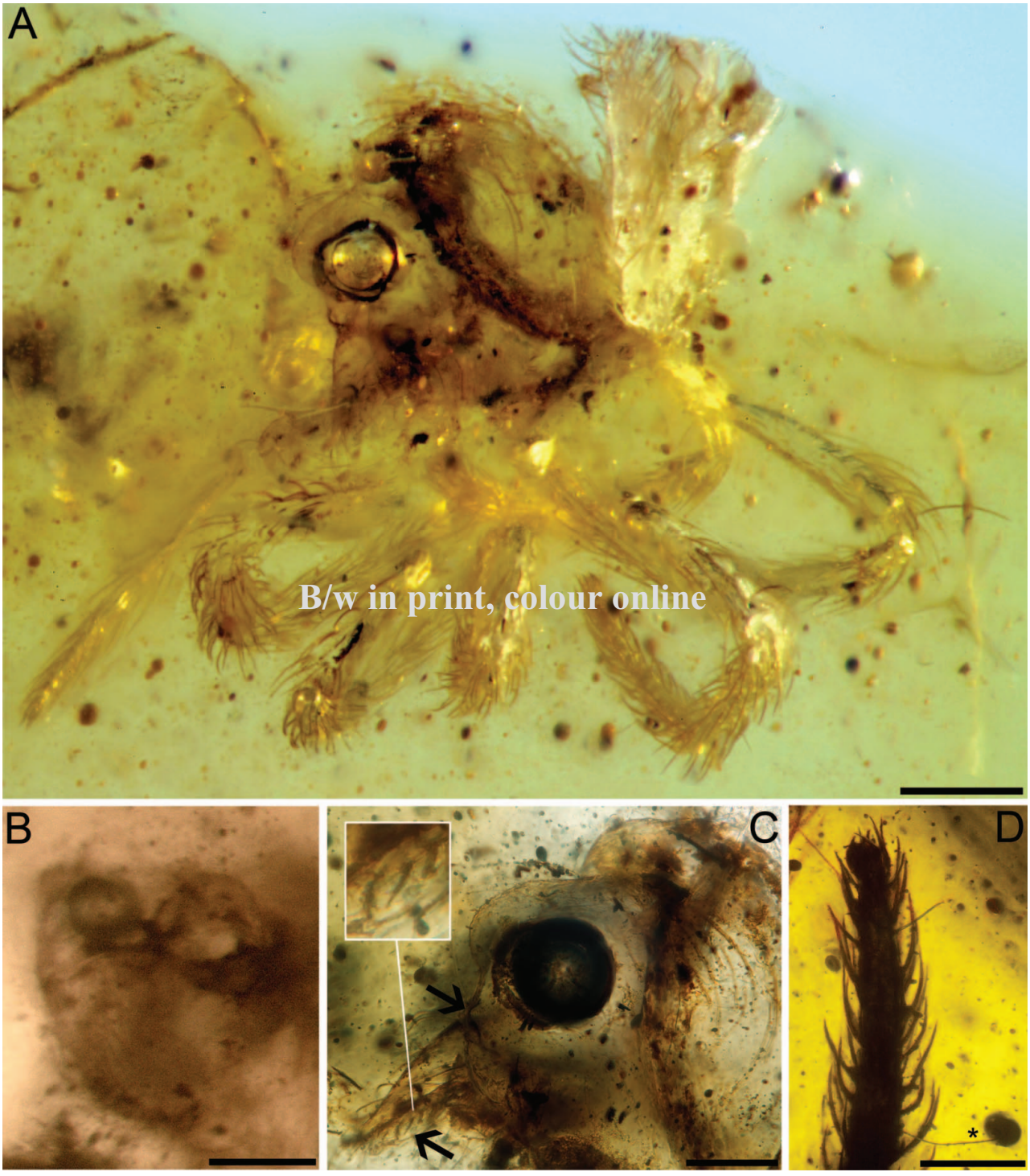

Figure 2. *Lagonomegops*? *cor* sp. nov., MCNA-13295; **A,** lateral habitus; **B,** dorsal view of the carapace; **C,** lateral view of the carapace; note the ALE/AME? (upper arrow) and cheliceral peg teeth (lower arrow), magnified in the detailed image; **D,** left mt and ts 4; note the elongated trichobothrium at distal mt and a tactile seta on distal ts. Scale bars: A, B = 0.2 mm; C, D = 0.1 mm.

Description. Body length not measurable but >1 mm long (Fig. 2A). Carapace compact, heart-shaped when viewed from above (Fig. 2B); very raised, with all sides steeply sloping but a more gradual slope towards posterior border; 0.52 mm long, 0.43 mm wide at widest point at about anterior third, 0.50 mm high. Cephalic region of carapace not distinct (anterior part of carapace not constricted or projected forward; no suture

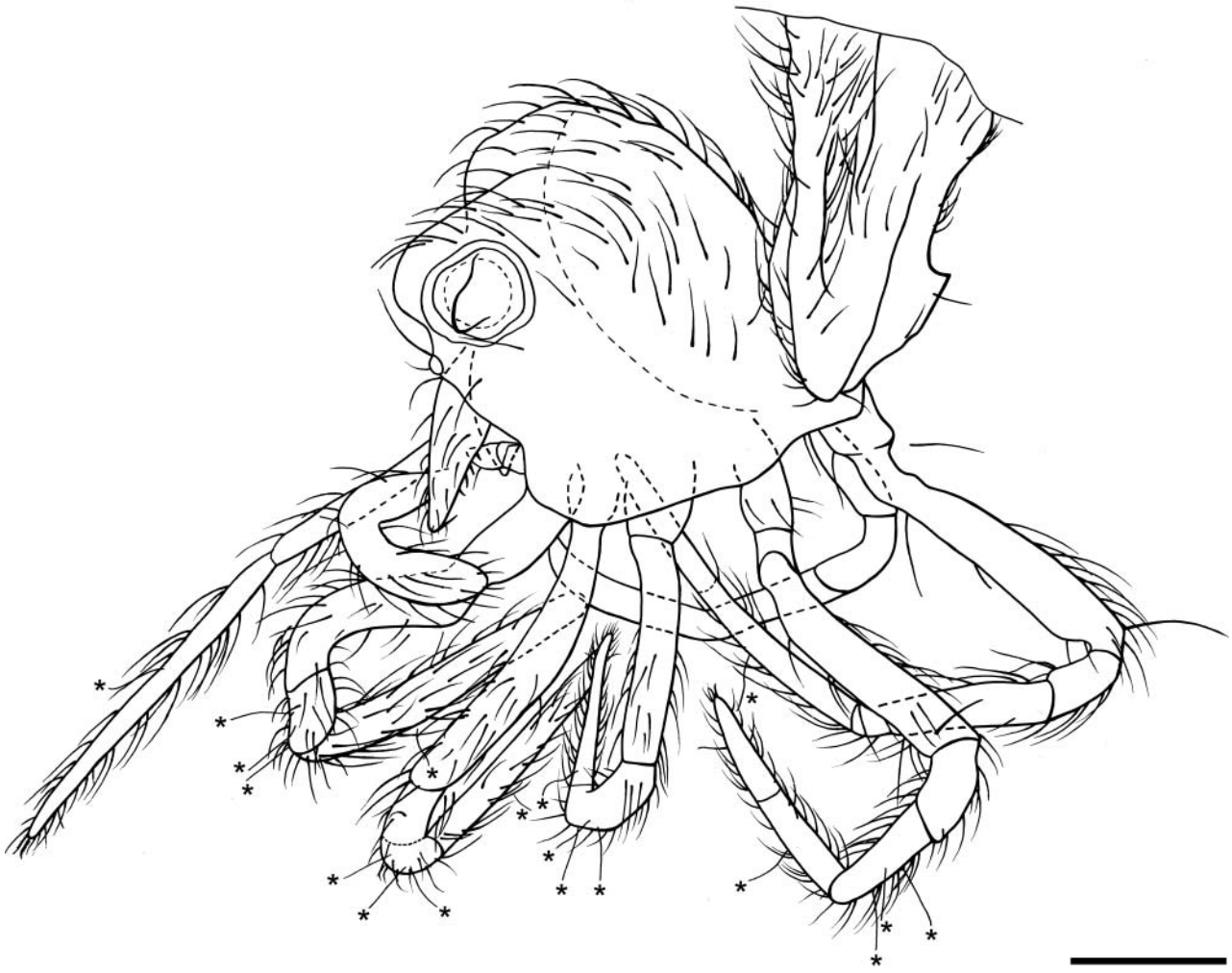

Figure 3. Camera lucida drawing of *Lagonomegops*? *cor* sp. nov. in lateral habitus, MCNA-13295; right legs 2–3 and setation of right leg 4 have been omitted to improve visibility. Scale bar = 0.2 mm.

delimiting the cephalic region from the thoracic region of the carapace). Anterolateral protrusions of the carapace large, >0.20 mm in diameter, occupying more than one-third of carapace length; frontal invagination created by the anterolateral protrusions very pronounced and acute (not rounded) (Fig. 2B, C), 0.11 mm long, 0.22 mm wide. Fovea absent. Carapace clothed in anteriorly directed, plumose setae, 0.09−0.11 mm long. Chelicerae subconical, gently procurved, anteriorly directed; 0.27 mm long, 0.12 mm broad at base; cheliceral insertion distinctly separated from the mouthparts in the vertical plane (i.e. chelicerae inserted at an elevated point of the carapace). Fang not visible. Ental margin of cheliceral unguis with four pointed, rather short peg teeth, 0.02 mm long (Fig. 2C). Cheliceral stridulatory files not visible or absent. Chelicerae covered with plumose setae, up to 0.08 mm long. Four eyes visible. PME 0.12 mm in diameter, situated on the anterolateral protrusions of the carapace, very faintly anteriorly directed if not completely laterally directed; strongly sclerotized ring around PME visible. ALE (AME?) around 3× smaller than PME, 0.04 mm in diameter, situated below the distal half of the PME, separated from the PME by slightly more than their diameter, close to the clypeal margin (Fig. 2C). Labium not visible. Endites elongated, subtriangular; serrula present. Sternum shape not discernible, but convex without tubercles and with plumose setae. Opisthosoma shrivelled, not measurable; not sclerotized; covered in plumose setae, 0.08−0.10 mm long. Spinnerets not preserved.

Legs relatively short and stout, no legs enlarged. Ts as long as mt or slightly shorter. Leg formula 4123/4213: leg 1 fe 0.34 mm, pt *c*.0.11 mm, ti 0.25 mm, mt 0.23 mm, ts 0.23 mm, total *c*.1.16 mm; leg 2 fe 0.33 mm, pt 0.11 mm, ti unknown, mt 0.20 mm, ts 0.20 mm, total >0.84 mm (ti lacking); leg 3 fe 0.30 mm, pt 0.11 mm, ti 0.16 mm, mt 0.16 mm, ts 0.14 mm, total 0.87 mm; leg 4 fe 0.36 mm,

pt 0.13 mm, ti 0.29 mm, mt 0.27 mm, ts 0.23 mm, total 1.28 mm. Three tarsal claws; paired claws 0.04 mm long, with six/seven teeth; median claw hook-like; onychium absent. Absence of setal scopulae or bristle-based, non-scopular structures on ts or mt 1 + 2. Legs covered in strong plumose setae, 0.08−0.10 mm long. Faint (almost hair-like in thickness), erect, curved, plumose, elongated bristle present on at least distal fe 1 + 3 + 4; 0.13−0.18 mm long. Tarsal trichobothria absent. Trichobothria dorsally on all ti and mt as follows: (1) Three on ti, two paired at two-thirds of its length and one at nine-tenths of its length, relatively elongated, 0.06−0.08 mm long; and (2) one at seven-tenths of mt, elongated to very elongated, 0.08−0.12 mm long (Fig. 2D). Tactile setae dorsally and ventrally on all mt and ts as follows: (1) one dorsally on distal mt, 0.06 mm long; (2) one to three dorsally on distal ts (Fig. 2D), *c.*0.05 mm long; and (3) up to three ventrally on distal ts, very short, 0.03 mm long.

Palpus slender; fe *c.*0.17 mm long, pt + ti 0.16 mm long, ts 0.18 mm long; bristles absent; with a long trichobothrium distally on palpal ti at two-thirds of its length, 0.11 mm long. Palpal claw absent. Plumose setae present, 0.08 mm long.

Remarks. The genus *Lagonomegops* is weakly delimited because the diagnosis is based on the absence of potentially apomorphic features present in other genera of Lagonomegopidae. Thus, *Lagonomegops* would clearly benefit from taxonomic revision if more data become available and clearer insight is gained into the phylogenetic relationships among taxa. With that said, MCNA-13295 is tentatively assigned to the genus *Lagonomegops* based on: (1) the absence of a distinctly raised cephalic region that projects forward as present in *Burlagonomegops* and *Soplaogonomegops* gen. nov.; (2) the lack of tarsal trichobothria (present in *Burlagonomegops* and *Spinomegops aragonensis* sp. nov.); and (3) the absence of cuticular specializations on the first two pair of mt and ts, i.e. the scopulae of densely arranged setae present in *Grandoculus* and the non-scopular bristles diagnostic of *Spinomegops* gen. nov.

Lagonomegops? *cor* sp. nov. differs from previously described species of *Lagonomegops* in possessing a carapace almost as long as high (length/height ratio close to 1; other *Lagonomegops* have carapaces not as high and distinctively longer). For example, the holotype of *L. sukatchevae* has a prosomal length/height ratio of 1.57, while the paratype has a ratio of 2.10 (Eskov & Wunderlich 1995). *L. americanus* has a similar prosomal length/height ratio of 1.92. Moreover, while the maximum height of the carapace is reached anteriorly in *L.*? *cor*, it is reached posteriorly in *L. sukatchevae* (Eskov & Wunderlich 1995, figs 3, 4). The anterolateral protrusions of the carapace are very prominent in *L.*? *cor* when compared to known lagonomegopid diversity, even more pronounced than *Grandoculus chemahawinensis* (Penney 2004, fig. 1A). On the contrary, in both *L. sukatchevae* and *L. americanus*, the anterolateral protrusions are faint (Eskov & Wunderlich 1995, fig. 1; Penney 2002, pl. 1.2). Finally, the ts are distinctly longer than the mt in *L. sukatchevae* (Eskov & Wunderlich 1995, fig. 7; Wunderlich 2008) but shorter or subequal in length in *L. americanus* (see measurements in Penney 2002) and the new species.

Genus ***Spinomegops*** gen. nov.

Type species. *Spinomegops arcanus* sp. nov.

Other species included. *Spinomegops aragonensis* sp. nov.

Diagnosis. Presence of numerous non-scopular (i.e. sparse, not arranged in dense rows), erect (almost perpendicular to the podomere), elongated (longer than regular leg setae), laterally disposed (both prolaterally and retrolaterally, not dorsally or ventrally), non-plumose bristles on distal metatarsi and tarsi of legs 1 + 2. Bristle thickness spine-like (*S. arcanus*) or almost hair-like (*S. aragonensis*).

Derivation of name. The epithet is the combination of *spina*, spine in Latin, after the diagnostic feature of the genus, and *Lagonomegops*, type genus of the family. The name is masculine.

Spinomegops arcanus sp. nov.
(Figs 4, 5)

Diagnosis. Carapace compact (not elongated), with maximum height reached posteriorly. Tarsal and metatarsal non-scopular bristles spine-like in thickness. Tibial trichobothrial pattern as follows: a single one at two-thirds of tibial length and another one subdistally, paired at least in legs 3 + 4. Spines on palpal tibiae and palpal tarsi present.

Derivation of ~~the~~ name. From the Latin adjective *arcanus* meaning hidden, secret or mysterious, referring to the inconspicuous shape of the specimen resulting from the cleared cuticle.

Material. MCNA-13307, juvenile or adult female from Álava amber, Peñacerrada I (= Moraza) outcrop, Burgos, Spain. The cuticle is cleared. The prosoma is distorted, and right legs 1 and 2 are badly preserved beyond the ti. Large bubbles are present inside the prosoma and opisthosoma, and additional ones occur inside the left PME and some leg segments. The spider is surrounded by organic debris.

Description. Body *c.*1.07 mm long (Fig. 4A). Carapace compact, oval when viewed from above; very raised, with lateral sides steeply sloping, posterior slope most likely steeply sloping; *c.*0.53 mm long, *c.*0.40 mm wide,

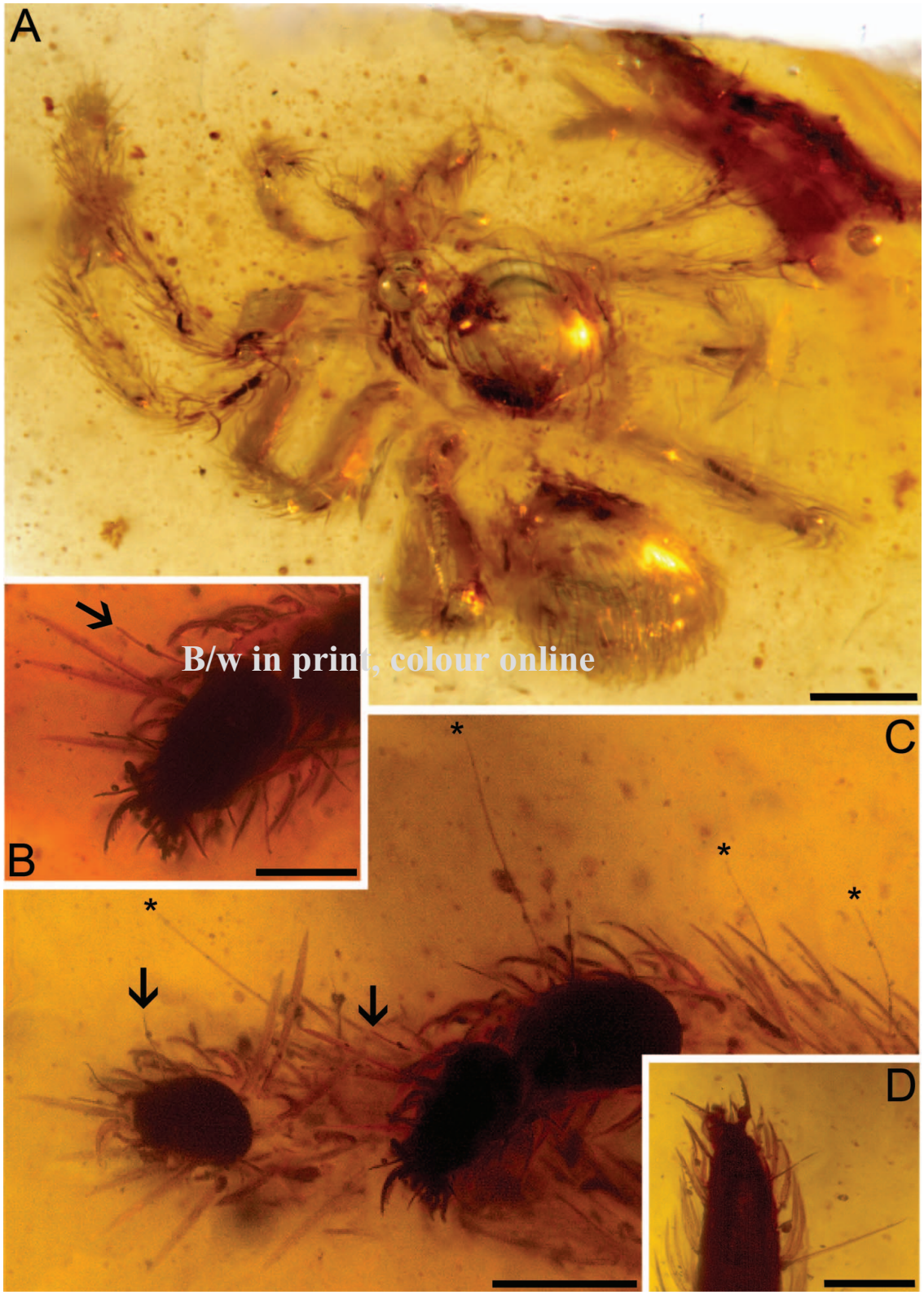

Figure 4. *Spinomegops arcanus* sp. nov., MCNA-13307; **A,** dorsal habitus; **B,** left ts 2 showing three retrolaterally disposed spine-like bristles and dorsal and ventral tactile setae; note the proximal hair-like structure tentatively interpreted as a tactile seta (arrow); **C,** distal podomeres of left legs 1 + 2, showing pro- and retrolaterally disposed spine-like bristles, tactile setae, and trichobothria; note the hair-like structures proximally on ts, tentatively interpreted as tactile setae (arrows); **D,** left ts 3; note the isolated basal bristle and the more dorsal tactile seta. Scale bars: A = 0.2 mm; B, D = 0.05 mm; C = 0.1 mm.

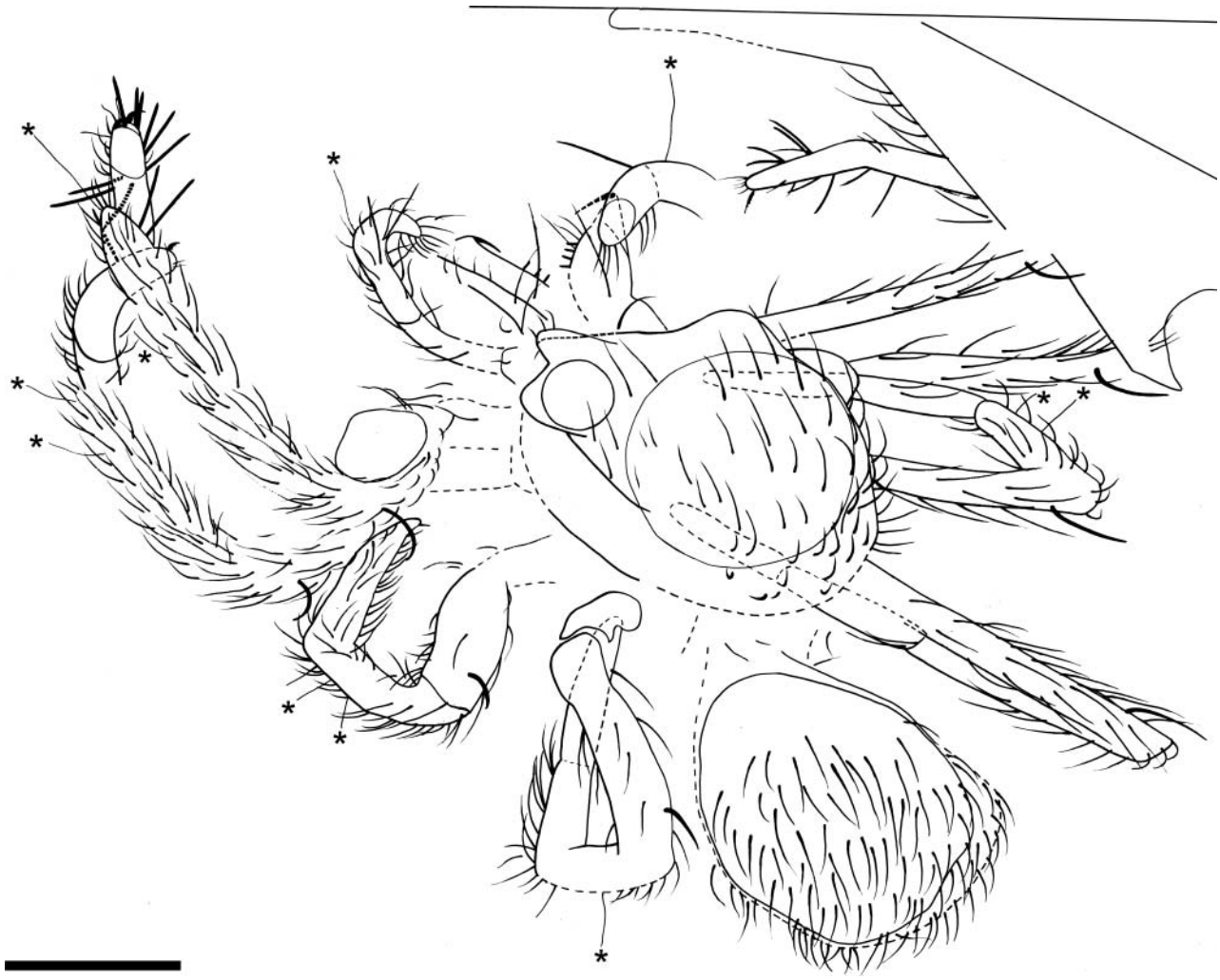

Figure 5. Camera lucida drawing of *Spinomegops arcanus* sp. nov. in dorsal habitus, MCNA-13307. Scale bar = 0.2 mm.

c.0.30 mm high (measurements approximate due to carapace distortion). Cephalic region of carapace not distinct (anterior part of carapace not constricted or projected forward; no suture delimiting the cephalic region from the thoracic region of the carapace). Anterolateral protrusions of the carapace apparently small, diameter not measurable; frontal depression created by the anterolateral protrusions slightly pronounced and rounded (not acute); 0.03 mm long, 0.25 mm wide. Fovea absent. Carapace clothed in anteriorly directed, plumose setae, *c*.0.05 mm long. Chelicerae subconical, anteriorly directed; 0.18 mm long, 0.08 mm broad at base; cheliceral insertion not discernible. Fang not visible. Ental margin of cheliceral unguis with four visible pointed peg teeth, 0.03−0.04 mm long. Single, erect, particularly elongated setae dorsoproximally on chelicerae, 0.14 mm long. Cheliceral stridulatory files not visible or absent. Chelicerae covered with plumose setae, up to 0.05 mm long. Only the PME visible, 0.14 mm in diameter; situated posterior to the anterolateral protrusions of the carapace; strongly sclerotized ring around PME present. Labium likely subtriangular, not measurable. Endites elongated, subtriangular, converging and almost meeting at the midline; 0.09 mm long, 0.08 mm wide at base, 0.03 mm wide at tip; serrula well developed, with a single row of teeth present that decreases in length distally. Sternum shield-shaped, convex; *c*.0.40 mm long, *c*.0.35 mm wide; marginal projections absent; without tubercles; covered in finely plumose setae. Opisthosoma ovoid, laterally compacted; 0.50 mm long, 0.20−0.30 mm wide, *c*.0.40 high; clothed in plumose setae, 0.08 mm long. ALS and PLS well developed; ALS ellipsoidal in section, 0.10 mm long, 0.12 mm wide, 0.07 mm high, separated by 0.05 mm; PLS subcircular in section, 0.09 mm long, 0.06 mm wide, separated by 0.13 mm. PMS not visible. Anal tubercle rhomboid in shape; *c*.0.04 mm long, 0.06 mm wide; covered in short, plumose setae, 0.04 mm long.

Legs relatively short and rather stout, no legs enlarged. Leg formula 2143/1243: leg 1 fe 0.37 mm, pt + ti + mt 0.60 mm, ts 0.23 mm, total 1.20 mm; leg 2 fe 0.42 mm, pt + ti + mt 0.57 mm, ts 0.20 mm, total 1.19 mm; leg 3 fe 0.31 mm, pt 0.05 mm, ti 0.19 mm, mt 0.19 mm, ts 0.19 mm, total 0.93 mm; leg 4 fe 0.40 mm, pt 0.06 mm, ti 0.23 mm, mt 0.23 mm, ts 0.19 mm, total 1.11 mm. Three tarsal claws; paired claws 0.03 mm long, with seven/eight teeth; median claw hook-like; onychium absent. Presence of numerous bristles on mt and ts 1 + 2, sparsely disposed (not forming scopulae), strong, i.e. clearly spine-like, in lateral position (both prolaterally and retrolaterally, not dorsally or ventrally), smooth (not plumose as the leg setation), subperpendicular regarding the ts; 0.08−0.12 mm long (Fig. 4B−D). Visible bristles are arranged as follows (bristles on right leg not detailed due to bad preservation, though clearly present): (1) left leg 1: two at the tarsal–metatarsal articulation, nine on ts apparently at two distinct points (two and two entally, two and three ectally); (2) left leg 2: five on ts. Bristles absent from ts or mt 3 + 4, except for a single one visible on ts 3 (Fig. 4D). Legs covered in plumose setae; 0.07−0.09 mm long. Erect, curved, plumose bristle present on all distal fe; *c*.0.12 mm long. Tarsal trichobothria considered absent (see discussion). Trichobothria dorsally on all ti and mt as follows: (1) two on ti, 0.06−0.09 mm long: one at two-thirds of its length and one at nine-tenths of its length (although, at least in legs 3 + 4, two paired trichobothria may exist at nine-tenths of ti length); and (2) one at four-fifths of mt, very elongated, 0.16 mm long, shorter in legs 3 + 4 (Fig. 4C). Tactile setae dorsally and ventrally on all mt and ts as follows (Fig. 4B−D): (1) one/two dorsally on distal mt, 0.05 mm long; (2) one dorsally at about one-half of ts 1 + 2, relatively elongated, 0.06 mm long; (3) up to four dorsally on distal ts (single in legs 3 + 4), 0.04 mm long; (4) a few ventrally on distal mt, relatively elongated, 0.06 mm long; and (5) up to four ventrally along all ts length, 0.04−0.05 mm long.

Palpus slender; fe 0.15 mm long, pt 0.08 mm long, ti *c*.0.13 mm long, ts 0.14 mm long; ti bearing at least two long, stiff, prolateral spines, one at about one-half of ti and one at about one-quarter of ts, 0.13 mm long; with a long trichobothrium on one-quarter of ti, 0.11 mm long. Palpal claw absent. Plumose setae present, 0.07 mm long.

Spinomegops aragonensis sp. nov.
(Figs 6, 7)

Diagnosis. Carapace elongated, with maximum height reached anteriorly. Eight eyes present. Tarsal and metatarsal non-scopular bristles almost hair-like in thickness. Tibiae with at least two short, paired trichobothria proximal to mid-length, and two longer trichobothria distal to mid-length. Single tarsal trichobothrium present. Spines on palpal tibiae and palpal tarsi absent.

Derivation of name. After Aragón, the Spanish autonomous community where the San Just outcrop is located.

Material. CPT-4155, juvenile or adult female from San Just amber, Teruel, Spain. The cuticle is cleared, which revealed characters that tend to be hidden, like the eyes and trichobothria. The distal portion of the opisthosoma and distal podomeres of leg 4 are not preserved. A large bubble is present inside the prosoma, and additional ones are present within some leg segments.

Description. Body 1.73 mm long as preserved (Fig. 6A). Carapace elongated, subpiriform when viewed from above; raised, with lateral sides steeply sloping and posterior sides moderately sloping (Fig. 6B); 1.02 mm long, 0.56 mm wide at widest point, *c*.0.55 mm high. Cephalic region of carapace distinct, projected forward, corresponding mostly to the anterolateral protrusions projected *c*.0.20 mm beyond the chelicerae insertion (Fig. 6B). Cephalic region not constricted, 0.43 mm wide distally, with two expanded, relatively narrow, anterolateral protrusions, *c*.0.35 mm in diameter; frontal depression created by the anterolateral protrusions pronounced and rounded (not acute), 0.06 mm long, 0.26 mm wide. No suture delimiting the cephalic region from the thoracic region of the carapace. Fovea absent. Carapace clothed in anteriorly directed, plumose setae, 0.10−0.12 mm long. Chelicerae subconical, procurved, slightly anteriorly directed (Fig. 6B); *c*.0.40 mm long, 0.20 mm broad at base; cheliceral insertion distinctly separated from the mouthparts in the vertical plane (chelicerae inserted at an elevated point of the carapace). Fang relatively stout, not measurable. Peg teeth not visible. Single, erect, particularly elongated setae dorsoproximally on chelicerae (Fig. 6B), 0.15 mm long. Cheliceral stridulatory files not visible or absent. Chelicerae covered with setae, not conspicuously plumose at least distally, 0.05 mm long. Eight eyes present. PME large (Fig. 6C, D), 0.16 mm in diameter; situated on the anterolateral protrusions of the carapace, slightly anteriorly directed; strongly sclerotized ring around PME visible. AME, ALE, and PLE 4× smaller than PME, 0.40 mm in diameter. AME and ALE contiguous, AME placed below ALE, with both situated below the distal half of the PME, close to the clypeal margin (Fig. 6C). PLE placed at the posterior margin of the anterolateral protrusions of carapace (Fig. 6D), separated 0.25 mm from the PME centre. Labium not visible. Endites elongated, subtriangular, converging and likely almost meeting at the midline; not measurable; serrula well developed, with a single row of at least 24 teeth. Sternum shield-shaped, relatively small, convex; *c*.0.43 mm long, 0.30 mm wide at widest point anteriorly, at about three-fifths of its length; marginal projections absent; distal end between cx 4 rounded. Opisthosoma ovoid, not sclerotized; 0.65 mm long as preserved, 0.58 mm wide, 0.55 mm high; clothed in

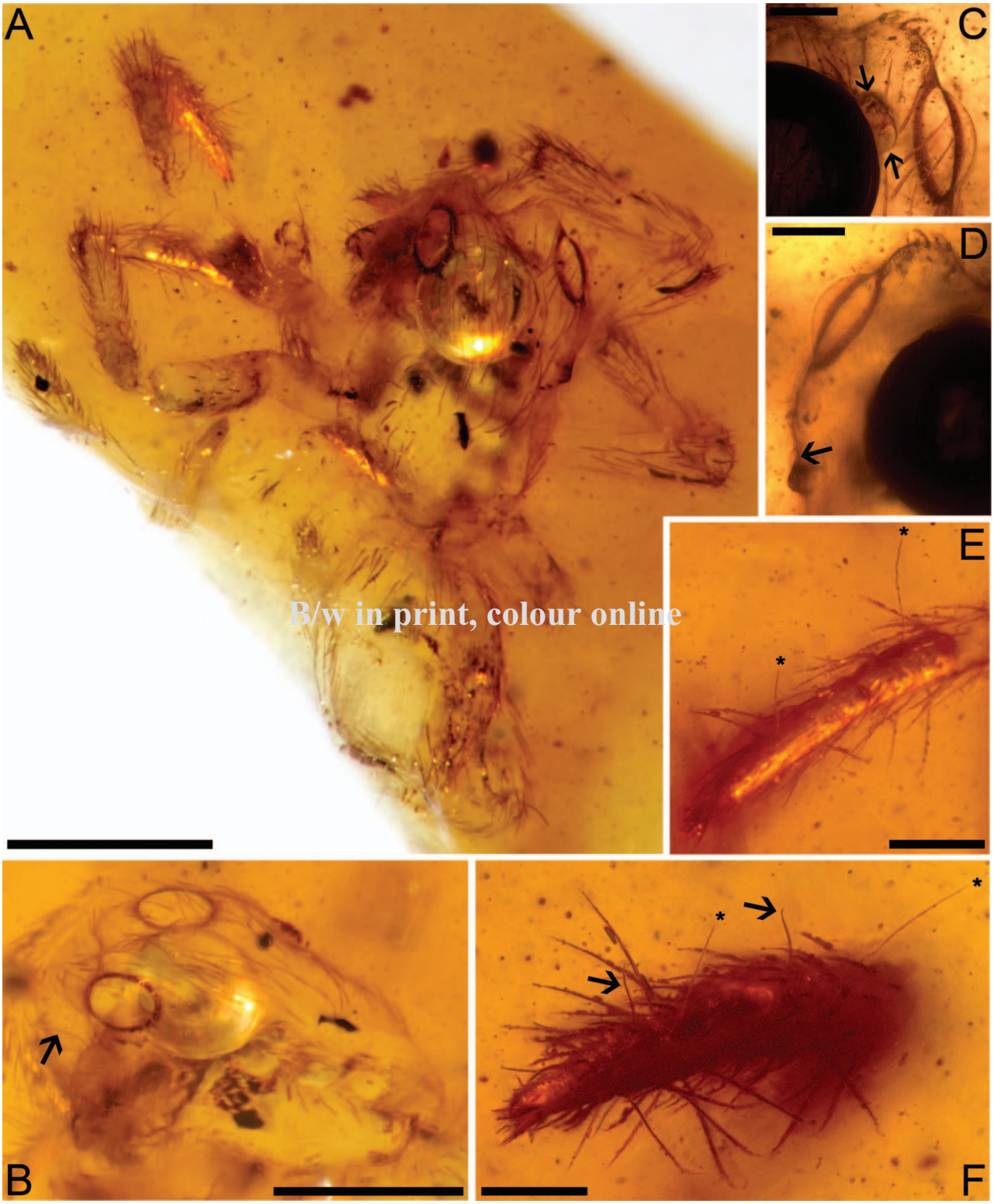

Figure 6. *Spinomegops aragonensis* sp. nov., CPT-4155; **A,** dorsal habitus; **B,** lateral oblique view of the carapace, showing the especially enlarged seta emerging from the dorsoproximal part of left chelicera (arrow); **C,** dorsal view of the right anterolateral protrusion of the carapace; note the AME (upper arrow) and the ALE (lower arrow) viewed through the cuticle; **D,** ventral view of the right anterolateral protrusion of the carapace, note the PLE (arrow); **E,** left mt and ts 2 showing some pro- and retrolaterally disposed bristles and trichobothria; **F,** left mt and ts 1 showing numerous pro- and retrolaterally disposed bristles, tactile setae (arrows), and trichobothria. Scale bars: A, B = 0.5 mm; C, D, E, F = 0.1 mm.

Figure 7. Camera lucida drawing of *Spinomegops aragonensis* sp. nov. in dorsal habitus, CPT-4155. The eyes have been tagged in the bottom left inset (setation omitted for clarity). Scale bar = 0.5 mm.

very faintly plumose setae, 0.10−0.12 mm long. Spinnerets not preserved.

Legs relatively short and stout, no legs enlarged. Ts as long as mt or slightly shorter. Leg formula 2143: leg 1 cx + tr 0.21 mm, fe 0.59 mm, pt 0.26 mm, ti 0.34 mm, mt 0.37 mm, ts 0.31 mm, total 2.08 mm; leg 2 cx + tr 0.26 mm, fe 0.63 mm, pt 0.23 mm, ti 0.39 mm, mt 0.33 mm, ts 0.33 mm, total 2.17 mm; leg 3 cx + tr 0.20 mm, fe 0.49 mm, pt 0.15 mm, ti 0.28 mm, mt + ts 0.44 mm, total 1.56 mm; leg 4 cx + tr 0.19 mm, fe 0.55 mm, pt 0.20 mm, ti 0.34 mm, mt + ts 0.56 mm, total 1.84 mm. Three tarsal claws; paired claws 0.04 mm long, with 7−8 visible teeth; median claw hook-like; onychium absent. Presence of numerous bristles on mt and ts 1 + 2, sparsely disposed (not forming scopulae), faint (not as strong as in MCNA13307), in lateral position (both prolaterally and retrolaterally, not dorsally or ventrally), smooth (not plumose as the leg setation), subperpendicular regarding the ts (Fig. 6E, F); 0.13−0.15 mm long. Visible bristles are arranged as follows: (1) right leg 1: one distally on mt and four on ts; (2) left leg 1: one on mt and *c.*10 on ts, starting beyond one-third of its length; (3) right leg 2: four distal on mt and *c.*10 on ts, starting beyond one-third of its length; (4) left leg 2: two on mt and three on ts, starting beyond one-third of its length. Bristles absent from ts or mt 3 + 4. Legs covered in weakly plumose setae, only clearly evident on fe; 0.11−0.13 mm long. Erect, curved, finely plumose bristle present on all distal fe; 0.09 mm long. Tarsal trichobothria present (Fig. 6E, F). Trichobothria dorsally on all ti, mt and ts as follows: (1) five on ti: two paired at about one-third of its length, very short, 0.04 mm long; two paired at about two-thirds of its length, 0.10 mm long; and one dubious distal one, 0.06 mm long; (2) one at about four-fifths of mt, very elongated, *c.*0.17 mm long; and (3) one placed slightly beyond ts mid-length, 0.10 mm long. Tactile setae dorsally and ventrally, at least, on mt and ts as follows (Fig. 6F): (1) one dorsally on distal mt, 0.06 mm long; (2) one dorsally slightly beyond one-half of ts, 0.06 mm long; and (3) a few ventrally along all ts length, *c.*0.03 mm long.

Palpus slender; fe 0.24 mm long, pt + ti + ts 0.45 mm long; with a thin, erect, slightly curved bristle-like setae dorsodistally on fe, 0.11 mm long; with a long trichobothrium on 7−8/10 of ti, 0.14 mm long, and an additional pair of shorter trichobothria, 0.07 mm and 0.05 mm long respectively. Palpal claw absent. Plumose setae present, 0.10 mm long.

Remarks. The new genus *Spinomegops* is diagnosed by the distinctive non-scopular structure composed of bristles present on mt and ts 1 + 2. We erect a new genus based on this character taking into account: (1) the taxonomic significance that has been granted to cuticular specializations on distal podomeres of the first two pairs of legs in Lagonomegopidae (i.e. the dense setal scopulae present prolaterally in *Grandoculus chemahawinensis* (Penney 2004, 2011; see Discussion) and Palpimanoidea (i.e. spatulate setae forming scopulae or not (Forster & Platnick 1984)), and (2) the morphological singularity of the described tarsal and metatarsal bristles found in MCNA-13307 and CPT-4155. Indeed, laterally placed (both prolaterally and retrolaterally) sparse bristles have not to our knowledge been described from any other known lagonomegopid or reported from any palpimanoid. These bristles are clearly stouter in *S. arcanus* sp. nov. than in *S. aragonensis* sp. nov. We recognize that our diagnosis lacks phylogenetic backing, but performing such analyses on lagonomegopids is difficult at present, considering outgroup choice is enigmatic at best, preservation of known diversity is often poor, and adults (at least males) are lacking ~~(see Discussion)~~. As such, our new genus and attendant diagnosis remains a hypothesis that can be overturned pending new analyses or data.

The presence of eight eyes in *S. aragonensis* confirms the presence of this character in the family, previously only reported as dubious from *Lagonomegops sukatchevae* (Eskov & Wunderlich 1995).

We assert that *S. arcanus* lacks tarsal trichobothria. However, even after applying the criteria used for discriminating between trichobothria and sensory or regular leg setae (see ~~Discussion~~), we found it challenging to discern the nature of the most proximal hair-like structure present dorsally on ts 1 + 2 (arrows in Fig. 4B, C). Tactile setae, which resemble in length and shape this hair-like structure, are also present ventrally on the distal mt and ts (Fig. 4C), and as such we consider the hair-like structure a tactile seta. This means, however, that within the same genus, one species has tarsal trichobothria whereas the other species lacks them. We acknowledge that this discrepancy may be taxonomically problematical, since the presence of tarsal trichobothria is currently the primary diagnostic character for the genus *Burlagonomegops*.

Genus ***Soplaogonomegops*** gen. nov.

Type species. *Soplaogonomegops unzuei* gen. et sp. nov.

Diagnosis. Cephalic region constricted in a neck that projects forward; chelicerae inserted at an elevated point of the carapace, clearly separated from the mouthparts in the vertical plane. Neck base with a semicircular suture. Cuticular specializations on metatarsi/tarsi absent. Tarsal trichobothria absent.

Derivation of ~~the~~ name. After the combination of El Soplao, the outcrop where the specimen was discovered, and *Lagonomegops*, type genus of the family. The name is masculine.

Soplaogonomegops unzuei sp. nov.
(Figs 8, 9)

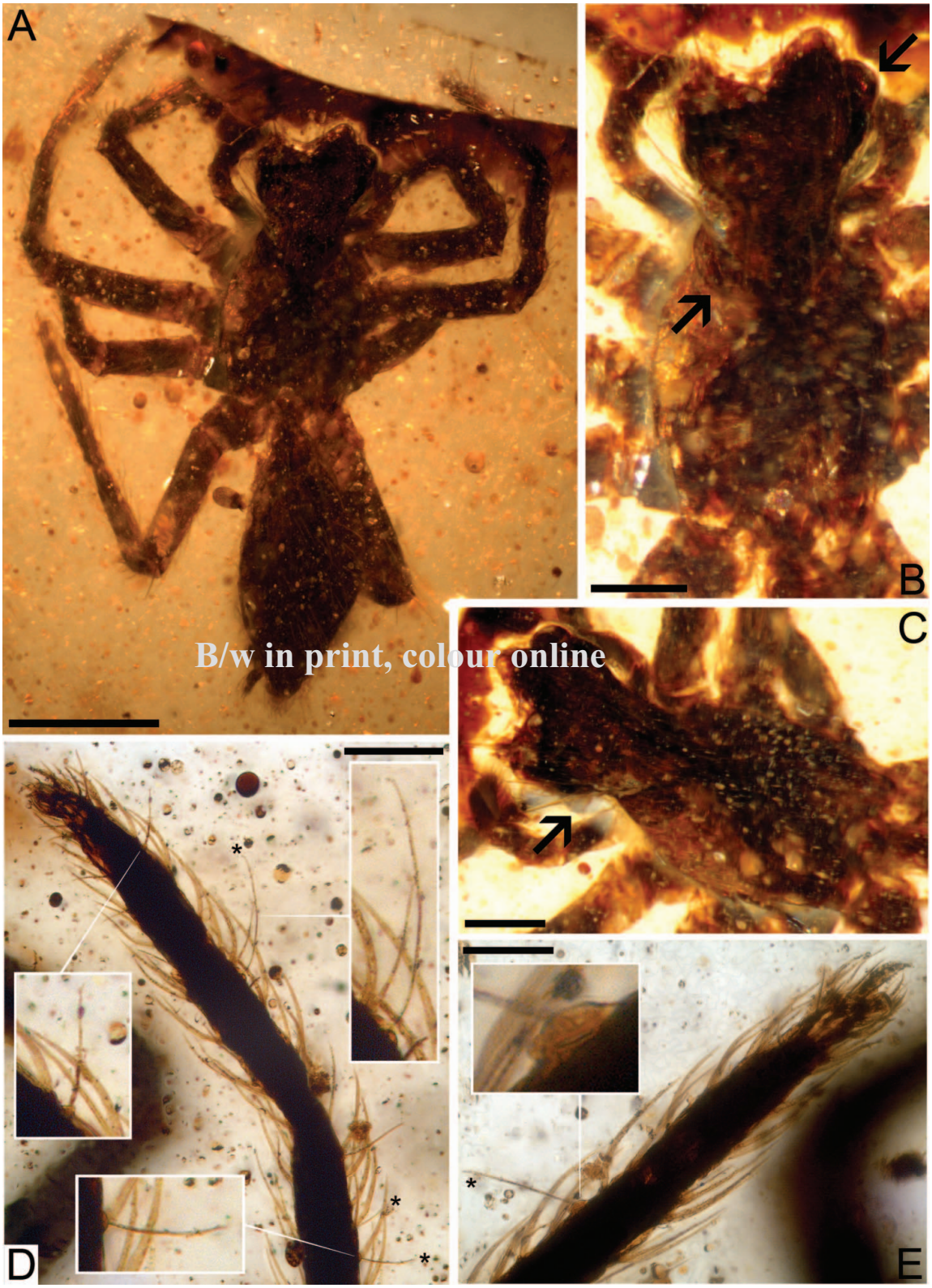

Figure 8. *Soplaogonomegops unzuei* gen. et sp. nov., CES-362; **A,** dorsal habitus; **B,** dorsal view of the carapace; note the PME (upper arrow) and the semicircular suture at the base of the neck (lower arrow); **C,** oblique view of the carapace; note the tip of the left chelicera (arrow); **D,** left ti, mt, and ts 2, showing trichobothria on ti (one is magnified at the bottom), a single trichobothrium on distal mt (magnified at the top right), and tactile setae (one magnified at the left); **E,** right mt and ts 2, showing tactile setae and a trichobothrium on distal mt with a very conspicuous bothrium (magnified in the detailed image). Scale bars: A = 0.5 mm; B, C = 0.2 mm; D, E = 0.1 mm.

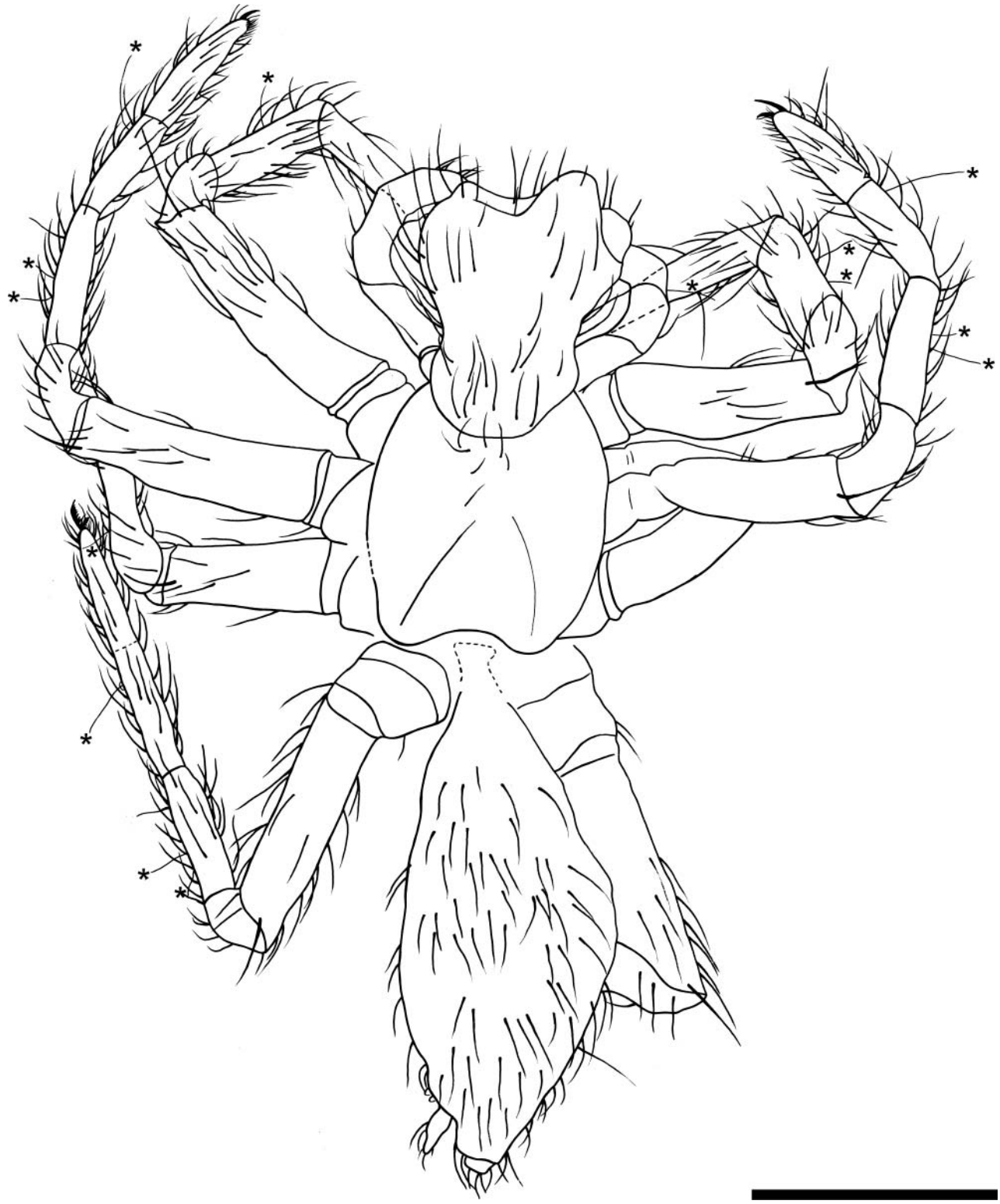

Figure 9. Camera lucida drawing of *Soplaogonomegops unzuei* gen. et sp. nov., CES-362. Scale bar = 0.5 mm.

Diagnosis. As for the genus (see above).

Derivation of name. The specific epithet is a patronym honouring Mr. Fermín Unzué, current manager of the El Soplao Cave, in recognition of his enthusiasm and interest in the study of El Soplao amber.

Material. CES-362, juvenile or adult female from El Soplao amber (Cantabria, Spain). The specimen has been preserved with high fidelity, although the thoracic region of the carapace has a posteromedial V-shaped depression that creates two acute, symmetrical posterolateral lobes (interpreted as artefacts caused by taphonomic pressure rather than a true character), and the anteroventral part of the opisthosoma is depressed. The amber piece contains abundant minute bubbles.

Description. Body *c*.2.10 mm long (Fig. 8A). Carapace very elongated (Fig. 8B, C); *c*.1.00 mm long, 0.49 mm wide at widest point at proximal third, height not accurately measurable but >0.40 mm. Cephalic region of carapace distinct, projected forward *c*.0.30 mm beyond the mouthparts and *c*.0.18 mm beyond the chelicerae insertion (Fig. 8C). Cephalic region constricted in a neck, with narrowest point medially; *c*.0.57 mm long, 0.25 mm wide at maximum width. Carapace slope decreasing at the base of the neck, where a semicircular suture delimits the cephalic and the thoracic regions of the carapace (Fig. 8B). Neck flaring out towards suture base. Anterolateral protrusions of the carapace relatively large, *c*.0.25 mm in diameter; frontal depression created by the anterolateral protrusions moderately pronounced and rounded (not acute), 0.07 mm long, 0.28 mm wide. Thoracic region of the carapace gradually rising towards the cephalic region, *c*.0.45 mm long. Fovea absent. Carapace clothed with anteriorly directed, plumose setae, up to 0.18 mm long. Chelicerae subconical, straight, barely posteriorly directed; 0.39 mm long, 0.22 mm broad at base; cheliceral insertion distinctly separated from the mouthparts in the vertical plane (chelicerae inserted at an elevated point of the carapace). Fang *c*.0.22 mm long. Ental margin of cheliceral unguis with three/four visible peg teeth, 0.05−0.07 mm long. Single, erect, particularly elongated setae dorsoproximally on chelicerae, 0.15 mm long. Cheliceral stridulatory files not visible or absent. Chelicerae covered with plumose setae, 0.06 mm long. Only the PME visible (Fig. 8B), 0.12 mm in diameter; situated on the anterolateral protrusions of the carapace, slightly anteriorly directed; strongly sclerotized ring around PME not conspicuous. Labium subtriangular, wider than long, with all apices rounded; 0.10 mm long, 0.13 mm wide at base. Endites elongated, subtriangular, converging and almost meeting at the midline; 0.18 mm long, 0.05 mm wide at base; serrula well developed. Sternum shield-shaped, slightly longer than wide; 0.41 mm long, 0.31 mm wide at widest point at about two-thirds of its length; marginal projections not evident; distal end between cx 4 rounded; without tubercles; covered in abundant setae. Opisthosoma elongated and narrow, not sclerotized; *c*.1.10 mm long, 0.42 mm wide as preserved, height not measurable; clothed in plumose setae, 0.09−0.13 mm long. Six spinnerets present in terminal position; ALS and PLS well developed, composed of two cylindrical segments, a larger proximal one, 0.10 mm long, 0.06 mm broad at tip, and a smaller distal one, 0.05 mm long, 0.03 mm wide; ALS close together; PLS separated by 0.14 mm; PMS small, 0.03 mm wide, length not measurable. Anal tubercle prominent, 0.04 mm long, 0.05 mm wide; covered in short, plumose setae, 0.05 mm long.

Legs relatively short, no legs enlarged. Ts shorter than mt. Legs 1, 2 and 4 subequal in length, so leg formula uncertain. Leg 3 the shortest. Leg 1 cx 0.07 mm, tr 0.13 mm, fe 0.42 mm, pt 0.15 mm, ti 0.24 mm, mt 0.32 mm, ts 0.30 mm, total 1.63 mm; leg 2 cx + tr 0.21 mm, fe 0.45 mm, pt 0.20 mm, ti 0.26 mm, mt 0.30 mm, ts 0.24 mm, total 1.66 mm; leg 3 cx 0.07 mm, tr 0.13 mm, fe 0.36 mm, pt 0.15 mm, ti 0.22 mm, mt 0.19 mm, ts 0.18 mm, total 1.30 mm; leg 4 cx + tr 0.18 mm, fe 0.49 mm, pt 0.16 mm, ti 0.27 mm, mt 0.27 mm, ts 0.26 mm, total 1.63 mm. Three tarsal claws; paired claws 0.05 mm long, with 12 visible teeth; median claw hook-like; onychium absent. Absence of setal scopulae or bristle-based non-scopular structures on mt and ts 1 + 2; a single ventral stiff bristle-like seta present on right mt 1 + 2. Two ~~of~~ visible stiff bristle-like setae prolaterally on right ts 2, single bristle-like seta visible retrolaterally on right mt 1 + 2. Legs covered in plumose setae, up to 0.12 mm long. Dense, short, sinuous plumose/serrated setae below the claws on all legs; 0.03 mm long. Faint (almost hair-like in thickness), erect, curved, plumose, bristle present on all distal femora; 0.18 mm long. Tarsal trichobothria absent. Trichobothria conspicuously plumose, dorsally on all ti and mt as follows (Fig. 8D, E): (1) two on ti, 0.10 mm long: one at four- to five-tenths of its length and one at six-tenths of its length, more proximally placed in legs 3 + 4; and (2) one elongated at eight-tenths of mt, 0.13 mm long. Tactile setae dorsally and ventrally on all mt and ts as follows (Figs 8D−E): (1) one dorsally on distal ti, 0.06 mm long; (2) one dorsally on distal mt, 0.06 mm long; (3) one/two dorsally on distal ts, 0.06 mm long; (4) at least, one ventrally on distal mt, 0.05 mm long; and (5) up to three/four ventrally beyond three-fifths of ts, very short, 0.04 mm long.

Palpus slender; fe 0.19 mm long, pt + ti 0.18 mm long, ts 0.17 mm long; bristles absent; with a long trichobothrium at seven- to eight-tenths of ti, 0.10 mm long. Palpal claw absent. Plumose setae present, 0.08 mm long.

Remarks. The distinct carapace morphology of CES-362 warrants erection of a new genus based on two ~~potential autapomorphies~~. First, the specimen is the only known lagonomegopid that possesses such a dramatic constriction of the cephalic region (i.e. neck). The cephalic region

can be constricted in the genus *Burlagonomegops*, but without forming a distinctive neck (Penney 2005, 2006), while constriction into a neck is only found within Palpimanoidea in some archaeids (e.g. Forster & Platnick 1984; Wood 2008). Second, the semicircular suture delimiting the cephalic region from the thoracic region of the carapace in *Soplaogonomegops unzuei* gen. et sp. nov. has not been described from any other lagonomegopid. Within Palpimanoidea, this character is highly diagnostic of the fossil genus *Spatiator* Petrunkevitch, 1942 from Baltic amber (Petrunkevitch 1942; Wunderlich 2004) but also present in some undescribed Baltic archaeids (pers. obs.). We note that the isolated bristles present on the mt and ts of legs 1 + 2 may be homologous with the numerous non-scopular bristles present in *Spinomegops*.

Discussion

Affinities of the family

Two characters, the presence of peg teeth and an elevated cheliceral gland mound, were used by Forster & Platnick (1984) as support for an expanded superfamily Palpimanoidea. This enlargement has been controversial, however, and some groups included by these authors have been removed based on subsequent molecular and morphological studies (e.g. Schütt 2000; Griswold *et al*. 2005; Rix *et al*. 2008; Rix & Harvey 2010). When Eskov & Wunderlich (1995) erected Lagonomegopidae, they placed the family in Palpimanoidea based on the combination of the following characters: (1) presence of peg teeth (Fig. 10A); (2) absence of (true) teeth on the cheliceral promargin; (3) nearly spineless legs; and (4) trichobothrial pattern (i.e. some trichobothria on the ti, even paired, a single one on the mt, and no tarsal trichobothria). The presence of peg teeth (character 1), although highly characteristic of Palpimanoidea (but absent in some groups such as Stenochilidae Thorell 1873), may be homoplastic and thus unreliable for systematic endeavours. For instance, peg teeth are present in some thomisids, periegopids and some mimetids (if the last are considered outside of palpimanoids) (Platnick 1976; Ono 1980; Forster & Platnick 1984; Platnick & Shadab 1993). True teeth (character 2) are lacking in many spider families (Jocqué & Dippenaar-Schoeman 2006). Characters 3 and 4 have been invalidated by subsequent lagonomegopid discoveries, as in the current paper. *Spinomegops* gen. nov. is characterized by the presence of numerous bristles on mt and ts 1 + 2, rendering character 3 variable. The trichobothrial pattern (character 4) can differ from that found within Palpimanoidea, i.e. a few on the ti and a single one (subdistal) on the mt (Forster & Platnick 1984). For example, the presence of tarsal trichobothria is currently one of the diagnostic characters for the genus *Burlagonomegops* (Penney 2005, 2006). The holotype and paratype of *B. eskovi* have ts with one long median and one short distal trichobothrium (Penney 2005), while *B. alavensis* possesses two to four trichobothria along all ts and more than a single (up to three) trichobothria on most mt (Penney 2006, fig. 2B). Although tarsal trichobothria are considered diagnostic, Wunderlich (2008) described several Burmese specimens attributed to *B.* ?*eskovi* that appear to lack this character. He also noted that the presence of tarsal trichobothria and more than a single trichobothrium on the mt would be exclusive within Palpimanoidea (cf. Forster & Platnick 1984). As such, Wunderlich (2008) regarded these trichobothria as non-trichobothrial hairs. Examination of the *B. alavensis* holotype (Fig. 10B, C) confirms the presence of numerous thin, very elongated, flexible, hair-like structures emerging perpendicular to the dorsal surface of the mt and ts of different legs. Since the shape of these structures mirrors the numerous trichobothrial hairs emerging from the ti (Fig. 10B), which are typical in lagonomegopids and the whole of Palpimanoidea (Forster & Platnick 1984), and fulfil the criteria detailed in the Material and Methods section, their status as trichobothria should be considered valid.

The above-mentioned four characters used by Eskov & Wunderlich (1995) for placing lagonomegopids within Palpimanoidea seem weak, and we refrain from identifying closest relative(s) for the group. Nevertheless, the diversity detailed herein revealed a variety of characters also found in palpimanoids, i.e. those characters concerning morphology of the carapace, eye arrangement, and presence of cuticular specializations on mt and ts 1 + 2, which are detailed below.

Carapace morphology. Two basic carapace morphologies can be distinguished within Palpimanoidea regarding point of cheliceral insertion: (1) true raising of the cephalic region, with chelicerae inserted at an elevated point on the carapace, resulting in clear vertical separation from the mouthparts (endites and labium) (see Forster & Platnick 1984); and (2) chelicerae not placed at an elevated point on the carapace, but rather close to the mouthparts vertically, at approximately the level of the sternum (pers. obs.). The former condition occurs in the palpimanoid families Archaeidae Koch and Berendt, 1854 and Mecysmaucheniidae Simon, 1895, while the latter occurs in the palpimanoid families Huttoniidae Simon, 1893, Palpimanidae Thorell, 1870, and Stenochilidae. The carapace shape is variable within Lagonomegopidae and, interestingly, both types of carapace morphologies co-exist. The first type, in which the chelicerae are inserted at an elevated point of the carapace, is present in the two species of *Burlagonomegops*, *Lagonomegops*? *cor* sp. nov., *Spinomegops arcanus* sp. nov., *Soplaogonomegops unzuei* gen. et sp. nov., and perhaps *Zarqagonomegops wunderlichi*, while the second type is present in *Grandoculus chemahawinensis* and *Lagonomegops sukatchevae* (see Eskov & Wunderlich 1995, figs 3, 4). We are unable to ascertain this character in *Lagonomegops americanus*.

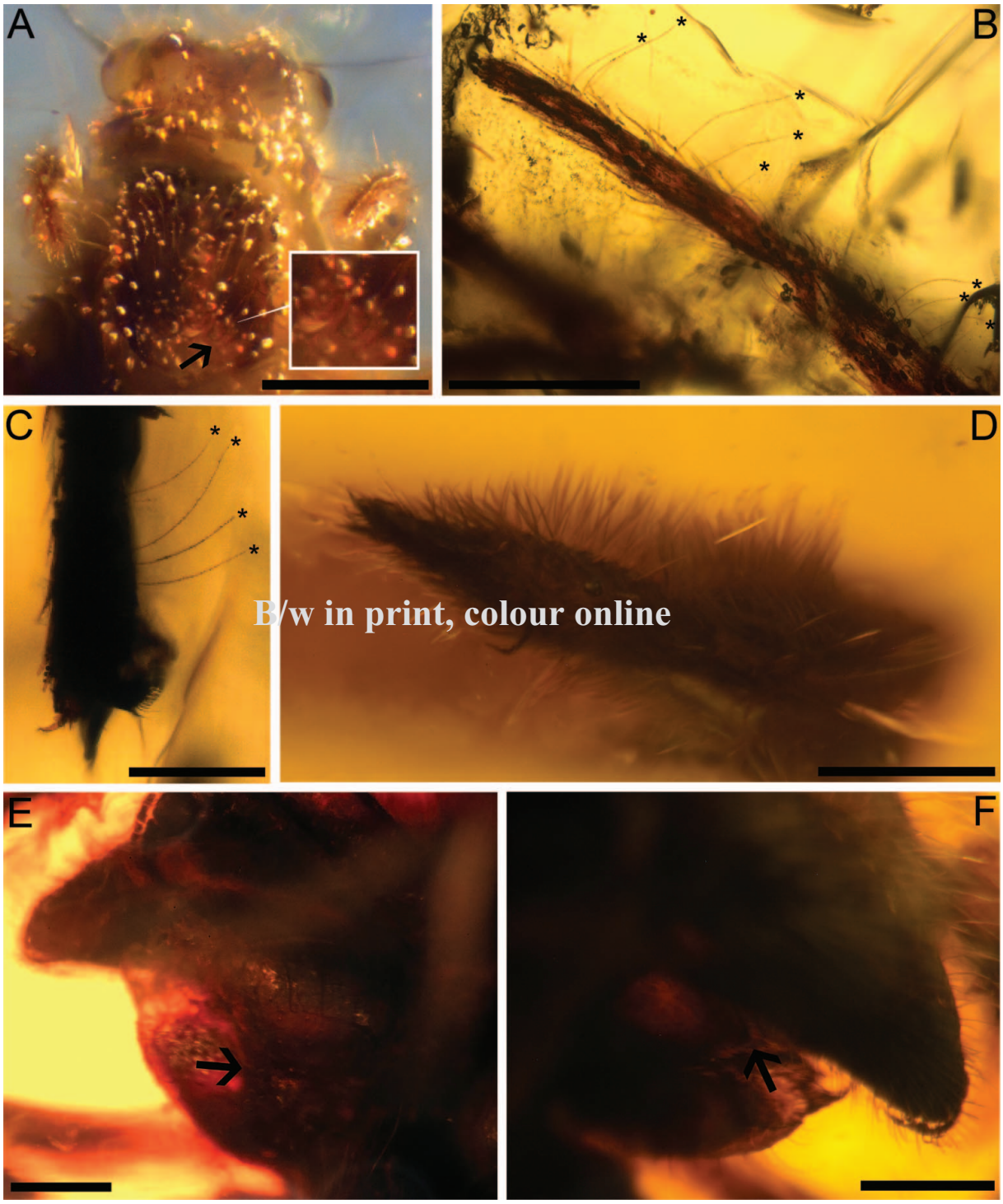

Figure 10. **A–C,** *Burlagonomegops alavensis* Penney, 2006, MCNA, holotype from Álava amber, Peñacerrada II outcrop (Álava, Spain); **A,** frontoventral view of the cephalic region of the carapace; note the pair of large PME and the four visible peg teeth on the cheliceral unguis (arrow), magnified in the detailed image; **B,** left ti (distal part), mt, and ts 3 and their visible trichobothria; **C,** distal part of left leg 4; note the presence of, at least, three tarsal trichobothria. **D–F,** *Grandoculus chemahawinensis* Penney, 2004, MCZ, holotype from Cedar Lake amber (Manitoba, Canada); **D,** prolateral scopulae of setae visible on left mt (right) and ts (left); note how the tips of the metatarsal scopular setae appear to be distinctly curved; **E,** ventral view of the anterior part of the prosoma, showing chelicerae (top left) and mouthparts (bottom right); the arrow marks the tip of the labium, where the endites meet at the midline; **F,** dorsal view of the anterior part of the prosoma, showing chelicerae (top right) and mouthparts (bottom left); the arrow marks the tip of the labium, where the endites meet at the midline. Scale bars: A, B = 0.5 mm; C, D, E, F = 0.2 mm.

Another prosomal trait present in lagonomegopids and also palpimanoids is the constriction of the cephalic region (neck) in *Soplaomegonops unzuei* gen. et sp. nov. found in archaeids (Forster & Platnick 1984; Wood 2008). Additionally, as mentioned, some Baltic archaeids have a semicircular suture delimiting the cephalic and thoracic regions of the carapace (pers. obs.), as occurs in *S. unzuei*. This character is also present in species of the palpimanoid genus *Spatiator*, currently classified as a family exclusively known from Baltic amber (e.g. Wunderlich 2006). Recent archaeids and some fossils may also possess a distinct cheliceral bristle on the proximal part of the chelicerae (Forster & Platnick 1984; Penney 2003), which is similar to the elongated, erect setae identified in *Spinomegops arcanus* sp. nov., *S. aragonensis* sp. nov. (Fig. 6B) and *S. unzuei*.

Eye arrangement. Eye homology is uncertain in lagonomegopids, and we tentatively employ the suggested nomenclature of Eskov & Wunderlich (1995). These authors assumed two recurved and very wide eye rows, with small and contiguous AME and ALE in the anterior row and a posterior row with large PME and small PLE well separated from the PME. Within Lagonomegopidae, eyes other than the large anterior eyes have been difficult to discern due to small size and variable position, often concealed by the anterolateral protrusions of the carapace. In the most recent diagnosis for the family (Wunderlich 2008), the presence of eight eyes was omitted, since six eyes were indicated for the genera *Lagonomegops* and *Zarqagonomegops*, while four eyes were noted for the remaining genera (*Burlagonomegops* and *Grandoculus*). Though eight eyes were described from *Lagonomegops sukatchevae*, the small eye below the PME (either the AME or the ALE) was considered dubious (Eskov & Wunderlich 1995). These authors noted that the lagonomegopid eye pattern seemed unique within Araneae. However, the eye conformation of *Spinomegops aragonensis* sp. nov. (Figs 6C, D, 7) (matching that of *Lagonomegops sukatchevae* if this specimen possessed eight eyes) resembles that found in Archaeidae (see Forster & Platnick 1984; Wood 2008), where the eyes are placed in two wide, laterally disposed eye rows, with a pair of anterior eyes the largest (although not as dramatically enlarged as in lagonomegopids) and two smaller, contiguous eyes placed below. The only significant difference between archaeid and lagonomegopid eye arrangement is that lagonomegopids have a posteriormost small eye (interpreted as the PLE) far beyond the other eyes, perhaps even in a separate, third row, whereas in archaeids the potentially homologous eye (considered the PME) is much closer. Roughly the same eye pattern as archaeids occurs in *Lacunauchenius speciosus* Wunderlich, 2008 from late Albian amber from Myanmar, placed within the subfamily Lacunaucheniinae Wunderlich, 2008 and closely related to modern archaeids and mecysmaucheniids (Wunderlich 2008).

Mouthparts. While the lagonomegopid eye pattern is potentially congruent with archaeids, their mouthpart morphology resembles that found in Mecysmaucheniidae. In both groups, the labium is wider than long, triangular, with the endites directed across the labium and almost meeting at the midline. Lagonomegopids, however, lack chelicerae originating from a foramen in the carapace, an important diagnostic character uniting Archaeidae and Mecysmaucheniidae (Forster & Platnick 1984).

Cuticular specializations on legs 1 + 2. Members of the genera *Grandoculus* and *Spinomegops* gen. nov. have cuticular specializations on the distal podomeres of legs 1 + 2, scopular in the former (composed of dense setae) and non-scopular in the latter (composed of sparse bristles). Within Palpimanoidea, the families Huttoniidae, Palpimanidae and Stenochilidae possess spatulate setae (specialized setae with an expanded distal plate) on distal podomeres of legs 1 + 2. These specialized setae form dense scopulae in Palpimanidae and Stenochilidae, whereas only a few rows are present in the Huttoniidae (Forster & Platnick 1984). Cuticular specializations on legs have been described from some modern archaeids, but representing just one or two rows of setae with slight lateral expansions (Forster & Platnick 1984). The scopulae of spatulate setae have been shown to improve the raptorial ability of spiders belonging to the genus *Palpimanus* (Palpimanidae) when hunting (Pekár *et al*. 2011), and prolateral spines with a raptorial function also exist in the Mimetidae (Platnick & Shadab 1993). Hence, perhaps the structures found in *Grandoculus* and *Spinomegops* were used for a similar function.

The family Grandoculidae

Penney (2011) erected the family Grandoculidae to accommodate *Grandoculus chemahawinensis*, previously considered a lagonomegopid by Penney (2004) (see also Penney & Selden 2011), using the following diagnosis: "[1] Raised cephalic region with a bulge on each side antero-laterally bearing a large eye [2] with a much smaller eye located below it; [3] chelicerae elongate and procurved. [4] Leg I distinctly longer and more robust than the others, with very closely packed, long, hook-tipped scopular hairs on the prolateral surface of the metatarsus, and long, straight, pointed scopular hairs on the prolateral surface of the tarsus (both these scopulae forming dense brushes); tibia of leg II with short scopulae along most of its length; [5] legs without spines and [6] palpal tarsus lacking a claw."

Features 1 and 6 are diagnostic of Lagonomegopidae. Penney (2011) indicated that character 2 distinguishes *G. chemahawinensis* from other lagonomegopids, including *Lagomegops sukatchevae*. Four eyes, however, are present (or, at least, visible) in *Burlagonomegops eskovi* and *Lagonomegops*? *cor* sp. nov., both of which lack scopulae. Regarding feature 3, *Lagonomegops*? *cor* and *Spinomegops aragonensis* sp. nov. have very similar

Table 1. Character distribution among lagonomegopid ~~spiders~~.

	Lagonomegops Eskov & Wunderlich, 1995	*Grandoculus* Penney, 2004	*Burlagonomegops* Penney, 2005	*Zarqagonomegops* Kaddumi, 2007	*Spinomegops* gen. nov.	*Soplaogonomegops* gen. nov.
Number of visible eyes	Up to 6 (8?)	4	4	6	Up to 8	2
Cephalic region projected forwards	Absent	Absent	Present	Absent	Present/absent*	Present
Cephalic region constricted	Absent	Absent	Present	Absent	Absent	Present (forming a neck)
Cephalic region semicircular suture	Absent	Absent	Absent	Absent	Absent	Present
Enlarged leg 1	Absent	Present	Absent	Absent	Absent	Absent
Cuticular specializations in legs 1 +2	Absent	Present (scopular)	Absent	Absent	Present (non scopular)	Absent
Tarsal trichobothria	Absent	Absent	Present	Absent	Present/absent*	Absent

*Present in *S. aragonensis*. See genus Remarks herein.

prosoma/chelicerae length ratios, around 2–2.5, and similarly procurved chelicerae, especially the latter species (Figs 2C, 6B). Character 5 is also invalidated after re-observation of the holotype, since an erect, curved spine is visible on left fe 1 (the specimen only has left legs 1–3 preserved beyond the femora). Furthermore, although not included in the diagnosis, the mouthparts of *G. chemahawinensis* were also employed as evidence for erecting the new family. Penney (2011) noted that the endites of *G. chemahawinensis* were not directed across the labium, and the latter was not triangular as in other lagonomegopids. Re-analysis of the holotype, however, revealed that the labium is, indeed, triangular, with two converging endites (Fig. 10E), as occurs in *Lagomegops sukatchevae*, type genus and species of the family Lagonomegopidae (Eskov & Wunderlich 1995, fig. 7). The right endite was likely misinterpreted as the labium by Penney (2004, 2011). Although barely visible in ventral view, the mouthparts of G. *chemahawinensis* can be seen in dorsolateral view (Fig. 10F). Additionally, although a single metatarsal trichobothria was described from *G. chemahawinensis*, some trichobothria, most likely arranged in two pairs, can be seen proximally on left leg 2. Consequently, the aforementioned features (1–3, 5–6) do not support granting *G. chemahawinensis* familial rank. Only feature 4 distinguishes *G. chemahawinensis* from other described lagonomegopids (Table 1), i.e. an enlarged first pair of legs and distinct cuticular specializations on legs 1 + 2, which correspond to hairs forming scopulae (= brushes) on the prolateral surface of mt and ts 1 (hairs hooked-tipped on the mt 1; Fig. 10D) and ti 2.

The two new species classified within *Spinomegops* gen. nov. are potentially related to *G. chemahawinensis* because they also have cuticular specializations on legs 1 + 2, i.e. numerous, elongated bristles (spine-like to almost hair-like in thickness) not forming scopulae (loosely arranged) on the pro- and retrolateral surface of the mt and ts 1 + 2. Nevertheless, we avoid classifying them within Penney's Grandoculidae or creating a new family because these taxa possess additional characters differentiating them from *G. chemahawinensis* and uniting them with lagonomegopids. Indeed, *S. aragonensis* clearly possesses eight eyes (Fig. 6C, D), the number reported as possibly present in *Lagonomegops sukatchevae* (Eskov & Wunderlich 1995, figs 3–4). Moreover, *S. aragonensis* has tarsal trichobothria and a raised cephalic region with chelicerae inserted at an elevated point in the carapace. Both of these characters are present in the genus *Burlagonomegops* which, in turn, lacks cuticular specializations on legs 1 + 2 (Table 1). Therefore, the presence of distinctive cuticular specializations on legs 1 + 2 may not warrant familial status, and we hypothesize these structures are homologous in the genera *Grandoculus* and *Spinomegops*.

While Penney may be correct in separating *G. chemahawinensis* from other lagonomegopids based on this character, elevating taxa to higher ranks seems prudent only when done in a phylogenetic framework (Penney & Selden 2011; Wiley & Lieberman 2011). Since the relationships within Lagonomegopidae and among potentially related taxa are not understood, we refrain from further splitting until more diversity is uncovered and/or quantitative analyses performed. We here consider Grandoculidae Penney, 2011 a junior synonym of Lagonomegopidae Eskov & Wunderlich, 1995.

Conclusions

With the taxa described herein, Spanish amber currently holds the greatest diversity of Lagonomegopidae. Our study supports the notion that lagonomegopid diversity was high during the Cretaceous, corresponding with a widespread distribution, at least in the Northern Hemisphere. Despite high diversity and a large geographical range, the group appears to have gone extinct by the end of the Cretaceous.

The placement of the family Lagonomegopidae within the superfamily Palpimanoidea remains controversial. The primary evidence supporting this affiliation is the diverse combination of important, possibly diagnostic, characters shared by lagonomegopids and different groups of palpimanoids. Our knowledge of these characters has been substantially improved with the taxa described herein. If lagonomegopids are considered palpimanoids, the lineage is most likely basal or sister to other palpimanoid lineages.

The family Grandoculidae is synonymized with Lagonomegopidae. The presence of cuticular structures on the legs does not warrant familial rank for *Grandoculus chemahawinensis*, as new taxa described herein possess this character and also present other characters diagnostic of lagonomegopids.

While the discovery of these fossils has increased our knowledge of Lagonomegopidae, it remains insufficient for a phylogenetic analysis of the family. A future assessment using taxa yet to be discovered will be essential for providing validity to existing genera and for testing the palpimanoidean nature of this group.

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Anexo I.11

Early evolution and ecology of camouflage in insects

Evolución temprana y ecología del camuflage en insectos

Referencia completa:

Pérez-de la Fuente, R., Delclòs, X., Peñalver, E., Speranza, M., Wierzchos, J., Ascaso, C. & Engel, M. S. 2012e, *reenviado a la revista tras informe favorable de revisores*. Early evolution and ecology of camouflage in insects. *Proceedings of the National Academy of Sciences USA.*

Resumen:

Los taxones pertenecientes a diversos linajes seleccionan y transportan materiales exógenos con el fin de camuflarse. Este comportamiento adaptativo también se da en los insectos, siendo los casos más conocidos las larvas de las crisopas. Éstas enmarañan la "basura" entre procesos cuticulares setosos, proceso que se conoce con el nombre de *trash-carrying*, que hace que sus depredadores y presas apenas los detecten, y también forma un escudo defensivo. Se presenta el hallazgo excepcional de una larva de crisopa en ámbar del Cretácico Inferior de España. Ésta presenta procesos cuticulares especializados formando una cesta dorsal, la cual alberga un denso *trash packet*. El *trash packet* sólo está compuesto por tricomas de helechos gleicheniáceos, los cuales indican la presencia de incendios en este ecosistema boscoso temprano. Este hallazgo representa una evidencia directa de la adquisición temprana de un conjunto de comportamientos que ha permanecido en estasis durante más de 110 millones de años, así como de una interacción antigua planta-insecto.

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Early evolution and ecology of camouflage in insects

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Author contributions: R.P.-F., X.D., E.P. and M.S.E. designed the study and performed research on the insect paleobiology, the plant-insect interaction, and camouflaging organisms; R.P.-F, M.S., J.W. and C.A. performed research on paleobotany; all authors analyzed data and discussed the results; R.P.-F. and M.S.E. wrote the paper.

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This article contains supporting information online at xxx.

Taxa within diverse lineages select and transport exogenous materials for the purposes of camouflage. This adaptive behavior also occurs in insects, most famously in green lacewing larvae who nestle the trash amongst setigerous cuticular processes, known as trash-carrying, rendering them nearly undetectable to predators and prey as well as forming a defensive shield. We report an exceptional discovery of a green lacewing larva in Early Cretaceous amber from Spain with specialized cuticular processes forming a dorsal basket that carry a dense trash packet. The trash packet is composed of trichomes of gleicheniacean ferns, which highlight the presence of wildfires in this early forest ecosystem. This discovery provides direct evidence of an early acquisition of a sophisticated behavioral suite in stasis for over 110 million years and an ancient plant-insect interaction.

Keywords. paleoethology | paleoecology | behavioral stasis | camouflage | plant-insect interactions

\body

Covering the body with actively selected exogenous materials as camouflage is a protective strategy occurring in invertebrate lineages as diverse as sea urchins, gastropods, crabs, and immature stages of insects (1). Given the great availability of 'trash' in the environment and the efficiency of such a defensive behavior, it be might expected that the origins of camouflage are ancient. However, like many behaviors, fossil evidence of such a complex defense is exceptionally scarce. The most famous examples of camouflage among insects are the specialized behaviors and associated morphologies in the larvae of green lacewings (family Chrysopidae and extinct allies, i.e. superfamily Chrysopoidea). Today Chrysopidae, with around 1200 species (2), are the second largest neuropteran family, having an almost cosmopolitan distribution and particularly abundant in tropical and warm habitats (3). Their campodeiform larvae are voracious predators generally living on trees, shrubs, and plants in a wide variety of ecosystems, and have been extensively studied as potential biological control agents in pest management programs (4, 5). These immatures often exhibit camouflaging behavior, known as trash-carrying, in which they harvest plant materials or even detritus and arthropod remains and carry them on their backs, nestled amongst cuticular processes specialized for the entanglement and transport of such debris. This trash packet camouflages the larva, preventing detection by predators and prey, and constituting a defensive shield in instances where the larva is attacked (6).

While the lineage of chrysopids has a moderately good fossil record extending into the Jurassic, with about 60 extinct species described, they are largely known from isolated compressions of wings and, more infrequently the full-body remains of adults (7). By contrast, fossils of their immatures are extremely scarce and the earliest definitive occurrences were from the Cenozoic (*SI Text*). The discovery of a complete larva in Early Cretaceous amber from Spain is therefore of considerable significance. Remarkably, not only does the specimen have the specialized morphological structures for carrying debris but its trash packet, comprising a

dense cloud of fern trichomes, is intact, demonstrating that the antiquity of the trash-carrying behavior extends to at least the Early Cretaceous, confirming previous predictions (8). This specialized camouflage strategy implies certain morphological and behavioral adaptations which are discussed, and more remarkably highlights the long-term stasis of this behavior in green lacewings, stretching over at least 110 million years. The nature of the fern trichomes, which originate from early colonizers after wildfires, used in composing the trash packet reinforces previous paleoenvironmental interpretations of the resiniferous forests as experiencing seasonal fires and perhaps stimulating resin production.

Systematic Paleontology

Order Neuroptera Linnaeus, 1758

Superfamily Chrysopoidea Schneider, 1851

Hallucinochrysa gen. nov. Pérez-de la Fuente, Delclòs, Peñalver & Engel

See Figs. 1, 2 and S1–S2 and Movie S1

Type species. *Hallucinochrysa diogenesi* sp. nov.

Etymology. From the Latin *hallucinatus*, 'illusion of the mind' after the bizarreness of the insect, and *chrysa*, a traditional ending of chrysopoid genus-group names, from *Chrysopa*. Gender: feminine.

Diagnosis (immature). Cephalic capsule banana-shaped, i.e. very broad and short with frons strongly concave. Presence of a coupling system at jaw apices. Median labial palpomere without annulations. Dorsum with pairs of setigerous, extremely elongate tubercles (= tubular tubercles); thorax with two pairs of tubular tubercles on each segment (lateral and laterodorsal pairs).

Hallucinochrysa diogenesi sp. nov. Pérez-de la Fuente, Delclòs, Peñalver & Engel

Etymology. A patronym for the Greek philosopher Diogenes of Sinope, whose name has been applied to a human behavioral disorder characterized by compulsive hoarding of trash.

Diagnosis. As for the genus.

Material. Holotype CES 418.1, from the Albian El Soplao amber site (*SI Text*), housed at the laboratory of the institutional El Soplao collection in El Soplao cave, Celis, Cantabria (Northern Spain). Larva, most likely a third instar, carrying a trash packet. Preservational and taphonomic characteristics of the sample are provided in the *SI Text*.

Remarks. *Hallucinochrysa diogenesi* possesses a bizarre, unique morphology, as the characters shown in the diagnosis are unknown from the extant green lacewing diversity. As most Neuroptera, all Recent trash-carrying green lacewings develop through three larval stages (9). Whereas first instars always show a low degree of setation and tubercle development, second and third instars reach the maximum tubercle length and setation (10). This suggests that *Hallucinochrysa diogenesi* represents an advanced larval stage, likely a third instar, despite the fact that the relative size of legs would be more typical of early instars. The existence of Early Cretaceous adult chrysopoids much larger than extant ones, also in the Barremian of Las Hoyas and El Montsec in Spain (7), make it difficult to use the total size of *H. diogenesi* as an inference regarding its ontogenetic development. The fossil has abundant fern trichomes (Fig. 3) entangled among setae of extremely well developed tubercles, forming a dense trash packet in the same fashion as modern trash-carrying chrysopids. A complete, detailed description and discussion of the systematic placement of the new taxon are provided in the *SI Text*.

Discussion

In Chrysopidae, apart from the morphofunctional type of larvae that exhibit the trash-carrying behavior, there are the so-called 'naked larvae', along with a few cases of morphologically and ethologically intermediate stages (11). Trash-carrying extant larvae tend to possess morphological characters that increase the potential for ensnaring debris as well as forming a defined space for the trash packet components (5). There is evidence that suggests that these adaptations evolved several times within Chrysopidae (12). Such adaptations are present in the fossil, as a gibbous (humped) body, adapted for moving while carrying great loads. However, two of these adaptations are strikingly peculiar. *Hallucinochrysa diogenesi* has: one, pairs of dorsal setigerous tubercles, but these are extremely elongate, tubule-shaped, and two, setation on the tubular tubercles, but representing a special system for ensnaring the trash packet components. In extant trash-carrying larvae, the lateral tubercles are often much more developed on the thorax than the abdomen, and the lengths of the thoracic tubercles never exceed the body width. By contrast, while those of the fossil are similarly developed on the thorax and abdomen, some of the preserved tubular tubercles not only exceed the body width but also the entire body length. Among the diversity of modified body setae observed in extant green lacewing larvae (5), setae with hooked ends or serrated along their rachis are the most specialized morphologies found for increasing the entanglement of the trash packet components. The morphology of the setae in the fossil represents yet another morphotype serving this same function. Similar setae occur in the neuropteran family Nymphidae (13). The trumpet-shaped setal endings (Figs. 1*C* and S1*E–F* and *SI Text*) act as anchoring points among surfaces of tangled trichomes, while the extremely fine distal portions of the setae facilitate the setae become flexible and to bend by gravity, enhancing their tangling and anchoring capacity. On the other hand, in extant larvae the trash packet is constructed from successive loads gathered with the jaws and placed on the dorsum by arching the head backwards while the thorax and abdomen are bowed forward (14, 15). The insect is also capable of reallocating the trash packet components with the jaws and abdominal peristaltic movements that cause movement from one set of bristles to contiguous sets (16). In the fossil trash packet there are clusters constituted by trichomes with the same or very similar orientation (Fig. 3*C–D*), indicating that they were pulled out together by the larva.

The extreme lengths of the tubercles suggest that *H. diogenesi* had its own, unique set of stereotyped movements used to construct the trash packet.

The trash packet plays an eminently defensive role against attackers, including cannibalism (5). Predators such as true bugs, ladybirds, ants, and parasitoid wasps have been reported as natural enemies of larval green lacewings (4, 16, 17), and this was likely true during the Mesozoic as well. The trash packet defense is two-fold (5, 15): first, its camouflaging properties prevent visual detection, also misleading predators by failing to properly recognize the larva during direct contact, and second, it acts as a physical shield. Hence, a plausible interpretation explaining the aberrant tubercle elongation of the present fossil is the function of special defense against predators with an elongate piercing/sucking proboscis, like true bugs, or parasitic wasps with elongate ovipositors.

Trash packets in extant larvae can be composed of a single debris source or various kinds of materials, and these can be of vegetal and/or animal origin. Animal trash packet components include invertebrate remains such as prey carcasses, insect exuviae (even their own), or snail shells, and also waxy secretions from aphids and mealybugs (14, 15, 18, 19). Non-animal elements include vegetal matter such as bark pieces, plant fibers, or leaf trichomes, as well as terrestrial algae, lichens, and other accidental elements like moss gametophytes, pollen, and fungal spores (16, 20, 21). *Hallucinochrysa diogenesi* gathered a packet solely consisting of plant trichomes (Figs. 3 and S3), suggesting co-specificity in respect to potential host plants. The trichomes are composed of an axis with a blunt base that corresponds to the trichome insertion, and 8–14 single, gradually-tapering secondary branches alternatingly inserted along a single plane (Fig. 3*A*–*C*). Opaque spheroid areas (OSAs) are distributed within the main axis at the point of insertion of secondary branches, sometimes slightly displaced from nodes. Trichomes are oval in cross-section (Fig. 3*C*), with a maximum thickness 30 μm, have a micropapillate surface, and a thick hyaline layer corresponding to cutinized cell wall (Fig. 3*E*–*G* and Movie S2). Trichome morphology includes variation as observed in extant individual plants, in part due to different stages of growth (*SI Text*). The overall structure corresponds to non-glandular, multicellular, branched, and dendritic trichomes (22, 23). We were able to positively identify the trichomes as of gleicheniacean ferns (Fig. S4 and *SI Text*), a lineage that comprises early colonizers in fire-prone environments (24). Ancient wildfires are promoters of resin production and accumulation, partially explaining the considerable abundance of amber in these coal deposits (25, 26) (*SI Text*). Interestingly, the particular branched morphology of the fern trichomes formed a more cohesive trash packet, hardly dislodgeable from the insect during movement. Additionally, trichomes also potentially provided the insect with a secondary, chemical defense against infectious agents, due to the presence of phenols on the cuticle surface as has been detected by autofluorescence signals (*SI Text*), reflecting a possible complex chemical ecology already present in the Early Cretaceous.

The trash packet's singular composition suggests that *Hallucinochrysa* larvae preyed on phytophagous arthropods (*SI Text*) living in gleicheniacean ferns. Based on the suggested specificity of the carnivorous larva with the plant host we infer a plant-insect interaction in which the structures produced by the plant to protect itself from herbivores are taken advantage of by a predatory insect to protect itself from predators. Today, this has been reported between an immature of a chrysopid species and the Arizona sycamore tree (16). Further evidence would be needed in order to consider this interaction as a result of a symbiotic relationship. Despite the dominance of gymnosperms in the arboreal composition of the paleoenvironment, the fern

affinity of the trichomes preserved in the trash packet harvested by the larva suggests that these insects actively sought plant materials from the understory rather than the trees most likely secreting the resin which subsequently entombed them.

In conclusion, we interpret the present fossil as a highly-specialized, probably derived, trash-carrying morphotype, rather than a primitive condition for modern green lacewings. The fossil represents one of the oldest direct evidences of camouflaging behavior in the fossil record, and the earliest known testimony of trash-carrying behavior for insects, greatly reinforcing the idea that Mesozoic green lacewing immature stages responded to similar adaptive pressures as did their Cenozoic counterparts (Fig. 4). The latter was first suggested when Cretaceous green lacewing eggs were found built upon stalks, a specialized strategy known from a very few living species for avoiding ant predation or parasitoids (27). On the other hand, it is clear that green lacewing immatures, like most holometabolan insect lineages, experience different selective pressures than their adults. For the green lacewings this would be particularly true during changes in vegetation. Some decisive changes occurred in the terrestrial paleoecology during the Early Cretaceous, when *Hallucinochrysa diogenesi* lived, mainly due to the incipient diversification of the angiosperms (28, 29). Extant green lacewing larvae mainly occur on gymnosperms and angiosperms (4, 5), which have a comparatively larger suite of phytophagous arthropods (30), but our finding suggests that, before the angiosperm radiation, ferns had a leading role in the evolution of trash-carrying in these insects.

Methods

The holotype was isolated within a small piece of transparent amber (13 x 9 x 5 mm) and embedded in a regular prism (23 x 15 x 5 mm) of epoxy resin (EPO-TEK 301) for optimal viewing and curation (31). An Olympus BX51 transmitted light microscope was used to study the insect in dorsal, ventral, and lateral views. Photography of the specimen employed both ColourView IIIu digital camera attached to an Olympus BX51 and Nikon D1x digital camera attached to an Infinity K-2 long-distance microscope lens. Nomenclature used for the insect description follows that of C. A. Tauber and co-workers (9, 32). Its reconstruction was undertaken in order to depict its aspect in life. The tridimensional model lacking setation was performed with LightWave 3D computer graphics program (NewTek). Movement patterns, body coloration, antennal length, and number of abdominal tubular tubercle pairs were reconstructed as in Chrysopidae representatives. Setation of tubular tubercles and several trichome clusters simulating an initial stage of a trash packet construction were added in the reconstruction image (Fig. 2). The trichomes were studied using a Zeiss Axio Imager D1 bright field/fluorescence microscope equipped with EC Plan-Neofluar 20x/0.50, Plan-Apochromat 40x/0.90 oil/glyc/water-immersion, and Plan-Apochromat 63x/1.40 oil-immersion objectives and using transmitted light with Köhler illumination. A CCD AxiocamHRc Rev 2 Zeiss camera and Carl Zeiss Axiovision 4.7 software were used to capture images of the trichomes. The autofluorescence signals from the trichome samples were observed with a Zeiss Axio Imager D1 microscope in the epifluorescence mode using EC Plan-Neofluar 20x/0.50 and Plan-Apochromat 40x/0.90 oil/glyc/water-immersion objectives. The microscope was equipped with a mercury lamp and specific filters for DAPI (Zeiss Filter Set 49; Ex/Em: 365/420–470 nm), eGFP (Zeiss Filter Set 38; Ex/Em: 450–490/500–550 nm), and rhodamine (Zeiss Filter Set 20; Ex/Em: 540–552/567–647 nm).

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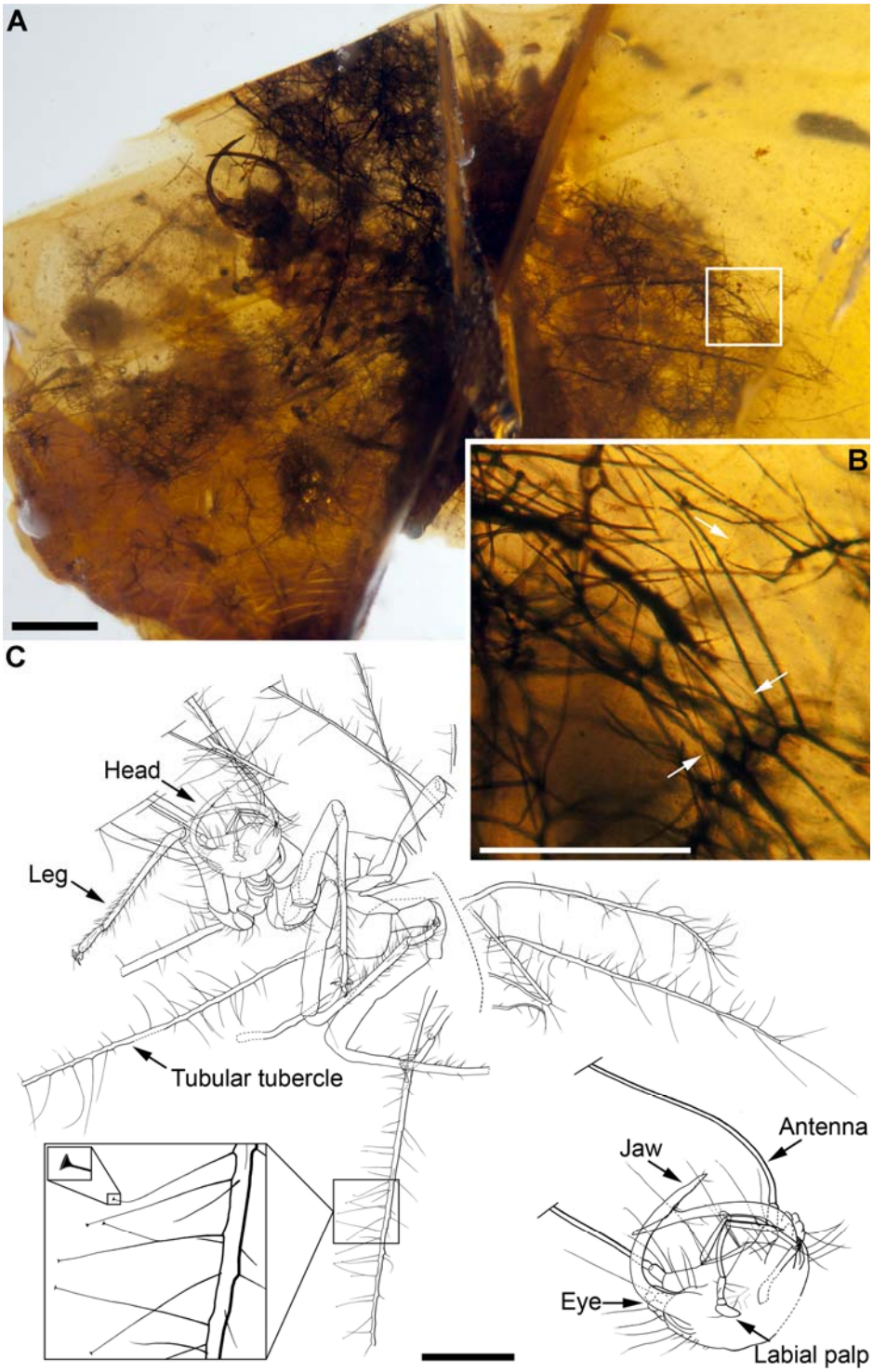

Fig. 1. Green lacewing larva with its dense trash packet composed of fern trichomes from the Early Cretaceous of Spain. (*A*) Photograph of *Hallucinochrysa diogenesi* gen. et sp. nov. (Neuroptera: Chrysopoidea) in ventrolateral view (holotype CES 418.1). (*B*) Close-up of box in *A*, showing enlargement of the apex of one abdominal tubular tubercle and some distal setae (arrows) trapping abundant trichomes. (*C*) Camera lucida drawing in the same view than *A*, but with a slightly different inclination; trash packet has been omitted for clarity and several tubular tubercles are obscured by the multiple main fracture of the amber piece. Bottom left inset noting the trumpet-shaped setal endings, and bottom right showing the head magnified. Scale bars 1 mm.

Fig. 2. Reconstruction of *Hallucinochrysa diogenesi* gen. et sp. nov. (Neuroptera: Chrysopoidea) in dorso-lateral view to show its life aspect. Trash packet reconstructed at an initial stage of construction. Head and leg setation have been omitted for clarity. Length of antennae, body coloration and number of abdominal tubular tubercle pairs based on extant larvae. Author: J. A. Peñas.

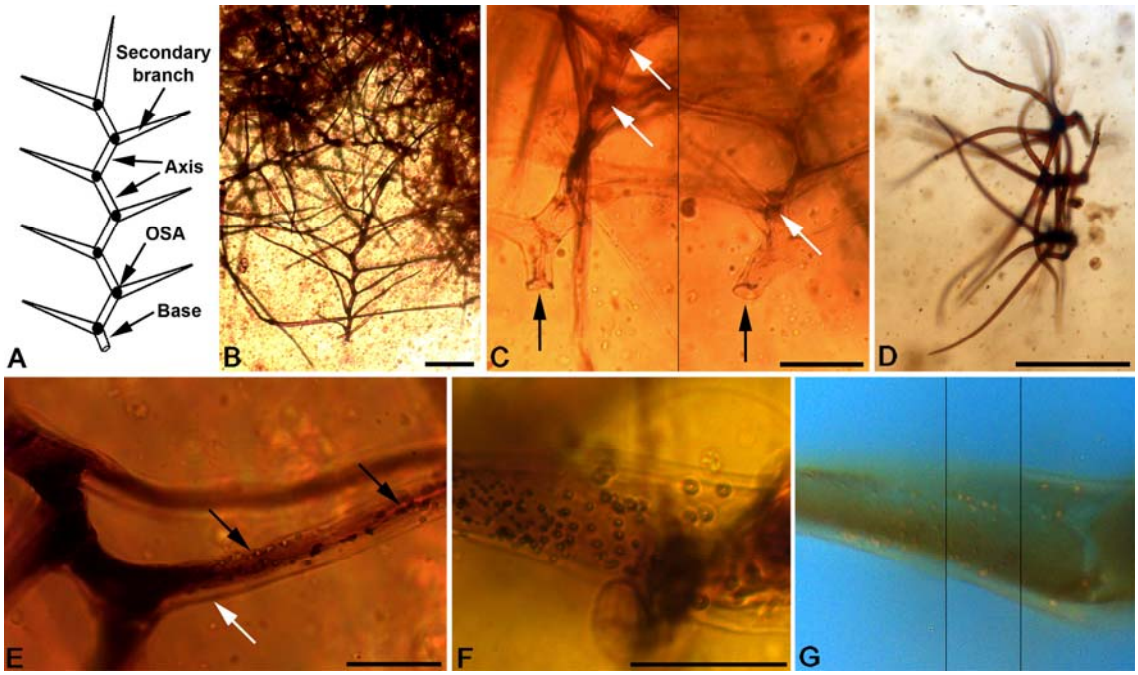

Fig. 3. Morphological features of the trichomes of gleicheniacean fern affinity from the trash packet. (*A*) Morphological parts outlined within text. (*B*) Large trichome at the limits of the trash packet. (*C*) Basal regions of two contiguous trichomes, composed from two focal planes, showing trichome bases (black arrows) and OSAs (white arrows). (*D*) Cluster of three trichomes at the same stage of growth and orientation that were pulled out together by the larva. (*E*) Detail of the trichome's cuticle and cell wall (white arrow) and micropapillae on the trichome's surface (black arrows). (*F*) Detail of micropapillate trichome surface under transmitted light microscopy. (*G*) Same detail that *F* under fluorescence microscopy, composed from three focal planes (at same scale that *F*). Scale bars = (*B*, *D*) 200 μm, (*C*) 50 μm, (*E*, *F*) 25 μm.

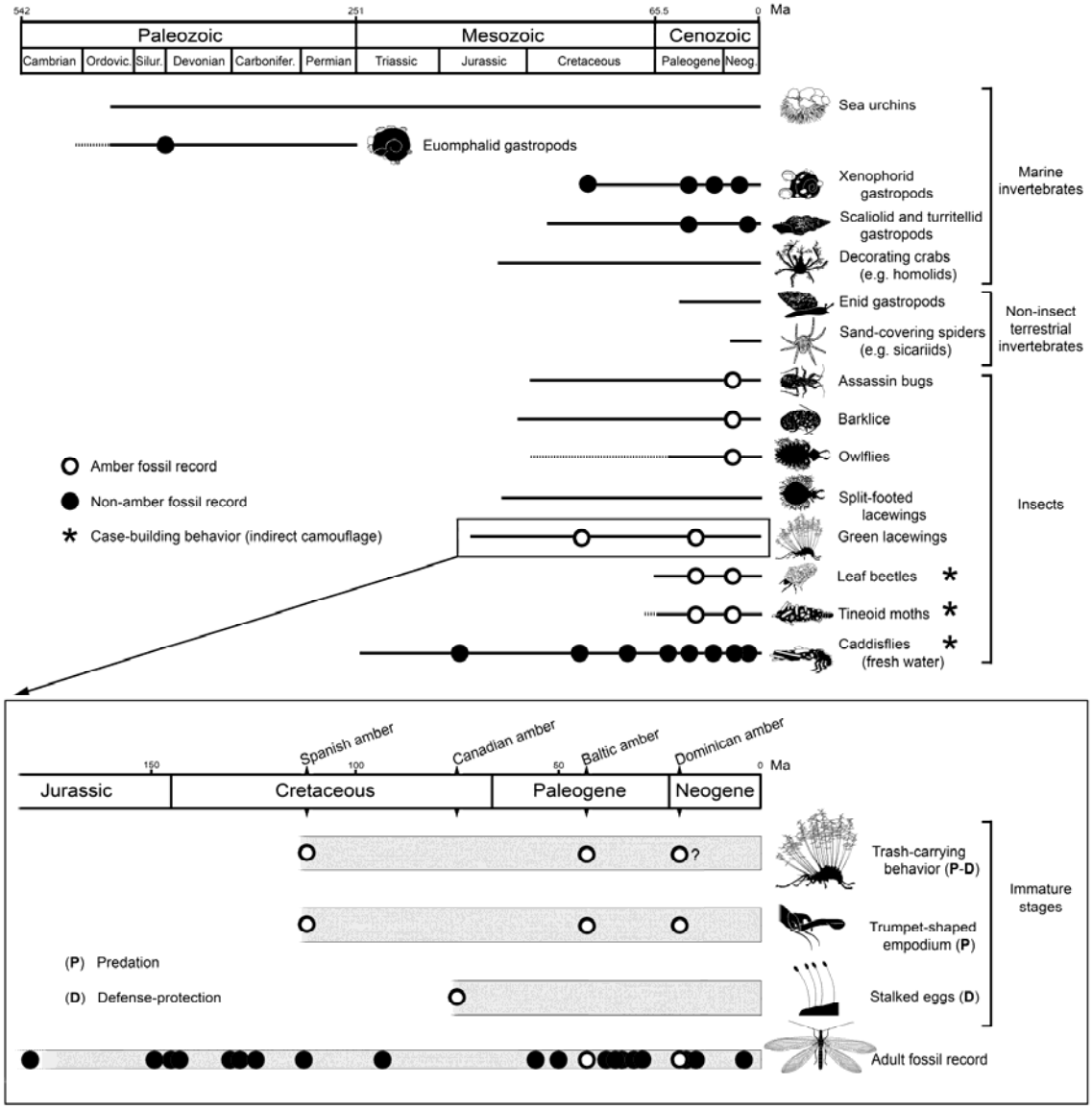

Fig. 4. Insect and other invertebrate groups in which the camouflaging behavior by actively harvesting and carrying exogenous materials is known, and their geological range. Direct fossil evidences of such behavior, when reported, have been marked with dots. The bottom box details the fossil evidence of the adaptations for predation and/or defense-protection present in the immature stages of green lacewings (family Chrysopidae and extinct allies, i.e. superfamily Chrysopoidea), and the geological range of the adult fossil record. The data used for this figure is provided in *SI Text*.

Supporting Information

SI Text

The insect, Hallucinochrysa diogenesi gen. et sp. nov.

Preservation and taphonomy. The holotype is almost complete, though both distal parts of antennae and some tubular tubercles are missing. A large, multiple amber fracture is crossing transversally the proximal part of the larval abdomen, thus several tubular tubercles are obscured. The cuticle preservation differs significantly between some parts, possibly reflecting different degrees of chitinisation: the head, legs, and tubular tubercles are very good preserved, but the thorax and the abdomen cuticle aspect is very weak. Tubular tubercles are preserved mainly erect, but a few of them are bent and/or partially collapsed in some portions. Apart from the larval specimen with its trash packet, the amber piece contains a brachyceran fly as a syninclusion (CES 418.2), suggesting that the resin exuded close to the branches in the aerial part of the plant where the larva gathered trichomes, instead of close to the ground.

The complete absence of air bubbles into the intricate, dense web that forms the trash packet of trichomes is indicative of emersion in a highly liquid resin. Nevertheless, the morphology and characteristics of other amber pieces from El Soplao are indicative of highly viscous resin. Apparently, both kinds of resin were produced by the same plant, most likely a cheirolepidiacean gymnosperm (33, 34). Because the resin of the piece in question was highly liquid and fossilized as clear amber, a detailed study of this complex bioinclusion has been possible.

Some parts of the larval body, mainly the tubular tubercles, contain pyrite deposits as thin crusts or clusters constituted by isolated cuboidal crystals (Fig. S1*A*, *C*, *D*). In the tubular tubercles, these thin crusts can obscure their real diameter (Fig. S1*D*). A few trichomes contain pyrite deposits as well. Pyrite mineralization in amber bioinclusions is not uncommon, mainly in Cretaceous ambers. That mineralization has been stablished in part as the origin of the exceptional preservation of diverse protist in Spanish Álava amber (35). The abundant presence of pyrite in the El Soplao organic-rich claystones , as in the other main Spanish amber outcrops, along with other evidences, indicates original suboxic conditions within the water-sediment interphase, where resins were originally deposited (36).

Description. Immature, probably a third instar. Body campodeiform, gibbous (likely moderately gibbous). Body length ca. 4 mm from head excluding jaws to apex of abdomen as preserved. Cephalic capsule banana-shaped, i.e. very broad and short with frons heavily concave, 1.00 mm wide. Jaws very long (ca. 1.20 mm), stylized and highly recurved; jaw apices with a few sensilla and serrate inner margins (Fig. S2*A*). Presence of a distal depression on ventral surface of right jaw and a conical process on dorsal surface of left jaw, both structures at similar distance from apexes, together interpreted as a coupling system (Fig. S2*B*). Palpiger with two setae. Labial palpi very gracile, having three palpomeres; basal palpomere with short setae except two extremely long setae at apex; median palpomere the longest (ca. 0.40 mm), without annulations; distal palpomere slightly club-shaped, bearing a terminal conical papilla

(0.31 mm including papilla) (Fig. S2*C*). Relative length ratio of median palpomere/distal palpomere 1.35 (i.e., lower than in extant larvae). Antenna gracile, fairly long despite missing distal parts; scapus elongate; pedicel cylindrical, 0.13 mm long; flagellum filiform, straight, with a constant diameter; flagellar base bulbous. Ocular tubercles very prominent, located on most distolateral sides of head, each with four stemmata (Fig. S2*D*). Several cephalic setae emerging from grooves, elongate (about as long as cephalic length) (Fig. S2*D*); at least five setae emerging from lateral sides of head, curving anteriorly, some elongate setae also present on longitudinal head axis. No apparent color pattern nor epicranial marks preserved. Cervix conical, elongate. Prothorax narrower than other thoracic segments. Setation on dorsal surface not conspicuous. Presence of extremely elongate, highly setigerous tubular tubercles on thorax and abdomen, apparently with same development. At least thorax with lateral and laterodorsal pairs of tubular tubercles on each segment (i.e., not simply one lateral pair) (Fig. S1*A*). Thoracic tubular tubercles with a broad insertion (Fig. S1*A*, *B*). Prothoracic pairs of tubular tubercles anteriorly directed (Fig. S1*A*), mesothoracic and metathoracical pairs more perpendicularly directed in relation to body axis. None of the thoracic tubular tubercles preserved in complete length, longest as preserved 3.64 mm; lateral and laterodorsal prothoracic tubular tubercles 0.08 mm and 0.09 mm wide, respectively. Tubular tubercles gradually thinner towards apices, at least abdominal pairs. Total number of abdominal tubular tubercles unknown due to the presence of a multiple fracture that obscures a large portion of the abdomen. Longest abdominal tubular tubercle over 4 mm long as preserved (incomplete). Tubular tubercles from anterior abdominal segments perpendicularly directed in relation to body axis and those from last segments posteriorly directed. Tubular tubercles with setae along entire length except the very base, shorter and sparser basally (setae of abdominal tubular tubercles about 0.40 mm basally and up to ca. 0.75 mm apically) (Fig. S1*E*). Tubular tubercle setae emerging from tuberculated bases more conspicuous towards the tubular tubercle apex (Fig. S1*C*), smooth (without serrations), strongly tapering apically, with trumpet-shaped endings (Fig. S1*E*, *F*). Legs distinctly large and robust; prothoracic leg 3.10 mm long (femur 1.18 mm, tibia 1.56 mm, tarsus 0.36 mm); mesothoracic leg 3.23 mm long (femur 1.49 mm, tibia 1.42 mm, tarsus 0.32 mm); metathoracic leg the largest, 3.68 mm long, total length estimated (femur 1.69 mm, tibia 1.60 mm estimated, tarsus 0.39 mm), about 1.2 times longer than prothoracic leg. Femora almost glabrous. Trochanters with a few long setae, with an external, rounded process on all legs bearing a particularly elongate seta. Tibiae and tarsi with copious setae, with a particularly elongate setae basally at each tibia. Tarsi with fused tarsomeres. Pretarsal claws long, sharp, recurved at an almost right angle (not curving inwards), with laminar basal expansions (Fig. S2*E*, *F*). Trumpet-shaped empodia well developed, 0.19 mm long (Fig. S2*F*, *G*). Two long, fine pulvilli between claws (0.19 mm long) (Fig. S2*F*). Last abdominal segment likely ending in a rather broad, depressed cone.

Phylogeny and fossil record of green lacewings and relatives. The superfamily Chrysopoidea comprises the extant family Chrysopidae and several allied, extinct lineages of lacewings. It is a matter of semantics whether these are all considered subfamilies within an expanded Chrysopidae s.l. or as families within a superfamily. Herein we prefer to consider the fossil lineages at the family rank (7), i.e., Mesochrysopidae Handlirsch, 1906, Limaiidae Martins-Neto & Vulcano, 1989, Allopteridae Zhang, 1991, Liassochrysidae Nel, Delclòs & Hutin, 2005, and Tachinymphidae Nel, Delclòs & Hutin, 2005. Chrysopoidea first appeared in the Lower Jurassic

and reached maximum disparity and geographical distribution during the Late Jurassic/Early Cretaceous (7). The extinct families, excluding Limaiidae, did not cross the K-T boundary. Chrysopoidea are closely related to the Hemerobiidae (7, 37, 38), or sometimes considered as allied to the Hemerobiidae and/or Osmylidae (39, 40).

The first adult fossil record relatable to Chrysopidae sensu stricto is *Paralembochrysa splendida* Nel, Delclòs & Hutin, 2005 from Late Jurassic/Early Cretaceous compression rocks in Liaoning Province, China. Other than that dubious record, modern Chrysopidae have been exclusively recognized from the Cenozoic fossils (7). The monophyly of Chrysopidae is well-supported, although relationships within the Neuroptera remain contentious (40–42). Significant advances have been made toward recovering stable relationships within the family (3, 43–45). Today, the majority of species of Chrysopidae belong to the subfamily Chrysopinae, which appeared during the Late Eocene. It has been suggested that, apart from their adaptation to the Cenozoic climate (46), the appearance and widespread distribution of the Chrysopinae since the Eocene is related to the evolution of their auditory organs (alar tympanic organs), which detect bat echolocation and permit escape responses (47, 48).

The fossil record of green lacewing larvae is extremely scarce. A green lacewing larva carrying a trash packet of ‘stellate hairs’ (oak trichomes) and other plant remains was figured from mid-Eocene Baltic amber, but without further study (49). Also, another green lacewing larva from Baltic amber, originally described as a hemerobiid (50), was recognized with some trichomes in the vicinity as possible remains of a trash packet, though the exemplar is lost (51). Furthermore, a described chrysopid larva from Early Miocene Dominican Republic amber lacks a trash packet (8). On the other hand, the only previously known Cretaceous record in amber of the lineage is a neonate first instar larva from Late Cretaceous Canadian amber (Campanian) which was entrapped while emerging from its characteristic stalked egg (27) (Fig. 4). In contrast, adult green lacewings are well-reported from impression/compression fossils (7), even though they are also outstandingly rare from amber deposits. In fact, up to now only three green lacewing adults have been described from the Dominican Republic amber (8), and another one has been reported from Baltic amber (52). No chrysopoid adults have been yet reported from Cretaceous amber. Therefore, the new discovery also represents the earliest record in amber of the superfamily Chrysopoidea.

Morphological comparison. Several studies have reviewed larval morphology and anatomy (4, 5, 9). The morphological disparity of *H. diogenesi* with both known extinct and extant chrysopid larvae is very remarkable. The larva figured from Baltic amber carrying a trash packet (49) lacks extremely elongate tubercles and legs are not particularly enlarged, whereas the larva described in 1856 by Hagen from Baltic amber, today lost, possessed ‘round, strongly constricted setigerous tubercles on the thorax’ (51), though it is not certain to which larval stage the specimen corresponded. The immature from Miocene Dominican amber (8) shows tubercles on the thorax and abdominal segments I–VII that are spherical. Each tubercle bears four to six very long, thick setae, which are inserted into conspicuous nodules from the tubercle. In addition, the head is subquadrate, the jaws are short and relatively blunt, and the legs are not particularly enlarged, being only slightly longer than the cephalic capsule plus jaws. Its scarce tubercle setation and small body size (1.3 mm) could indicate that it was a first instar. Regarding the neonate reported from Late Cretaceous Canadian amber preserved as it emerged

from its stalked egg (27), no other features are preserved to permit a more conclusive determination as to its later morphology, behavior, or ecology. Today, neonate larvae, after hatching through a slit formed at the egg cephalic pole by its egg-burster, remain clung to their stalked egg for several hours until the body hardens and the jaws become operative (4), probably explaining this exceptional record.

Modern chrysopid larvae have palpi with a short basal palpomere, an annulated second palpomere distinctly more elongate than the others, and a shorter third palpomere slightly tapering distally (9). However, the three palpomeres of *Hallucinochrysa diogenesi* are not so different in length, the annulations of the second palpomere are not present, and the elongate third palpomere does not taper distally but slightly expands. Also, the bizarre tubercle length as well as the special cephalic capsule morphology of *H. diogenesi* (i.e. banana-shaped head) are not found today in extant green lacewing diversity, even though they could represent highly variable characters because today they strongly depend on trash-carrying and feeding habits, respectively. Lastly, the coupling system of the jaws has not been described, to our knowledge, from any Recent chrysopid larvae.

Suprageneric-level assignment. The most conservative is to classify *Hallucinochrysa diogenesi* as a Chrysopoidea of uncertain family. Exclusion of *H. diogenesi* from Chrysopidae sensu stricto is supported by the fact that, even though it shows the same bauplan that extant trash-carrying chrysopid larvae, it exhibits several unique characters, as noted above. Also, Chrysopidae sensu stricto are not recognized until the Cenozoic (7). It is interesting to note that the current high-level classification within Chrysopidae is almost only based on adult characters (3), as parallelisms and convergence in larval traits are rampant across the family (12). However, larval anatomy and morphology have proven to be of great importance for recovering lower-level relationships within the family (53, 54).

On the other hand, it is not possible to assign the fossil to any extinct chrysopoid family because nothing was previously known about the larval stages of non-chrysopid chrysopoids. Although there is evidence of the extinct chrysopoid families Allopteridae and Tachinymphidae living in the Iberian Plate during the Early Cretaceous, i.e. adult rock fossils (7), it is virtually impossible to relate adult forms with their larval counterparts.

Predatory habits. While chrysopid adults have mainly carnivorous diets or feed on plant products, larvae are always voracious predators and mostly polyphagous, but sometimes stenophagous (4, 18). As is true for all immature neuropterans, chrysopid larvae have sucking jaws, which inject salivary secretions and then absorb the liquified tissues and internal fluids (4). The common prey of extant green lacewing larvae are sternorrhynchans such as aphids, coccoids, and psyllids, but the prey range covers an extreme diversity of groups, including spiders, phytophagous mites, and other insects such as hemipterans, thrips, barklice, hymenopterans, or even termites (5), the majority of which are represented in Spanish Albian ambers (25). The potential diet of the fossil larva can be delimited. First, aphids, the main food for extant green lacewings, were extremely scarce in its paleoenvironment in comparison with coccoids, the relative abundance of which has been explained by the low paleoclimate seasonality (55). Second, insects associated with extant ferns are mainly hemipterans, beetles,

and lepidopterans, with a high proportion of sap-feeders and specialist feeders restricted to ferns; it has been estimated that only 9,300 insect species are able to use ferns as a food source, compared to approximately 400,000 species of insects that use angiosperms (30). In addition, it has been demonstrated that the jaw length and cephalic width, which relates to more widely-spaced jaws, are related with prey size (56); thus, the very long jaws of *Hallucinochrysa diogenesi* (ca. 1.20 mm) and its especially broadened cephalic capsule suggest specialization or, at least, capacity to feed on large prey. The trumpet-shaped empodia allows an efficient anchoring to the substrate that is associated with not only better locomotion but also an increase of the ability to capture and retain active prey (57).

Trichomes from the plant host

Overview on trichomes. The filamentous plant remains composing the larval trash packet are recognized as plant trichomes due to their morphology, size range, micro-ornamentation, and autofluorescence signals. Trichomes exhibit the greatest diversity of intra- and interspecific morphological variation among plant epidermal outgrowths, ranging from a few micrometers to several millimeters. Hundreds of different trichome morphologies have been documented from vegetative and reproductive structures of diverse vascular plants, having long been used for taxonomic purposes (22, 58–60). According to their function, trichomes can be glandular or non-glandular and are characterized by numerous anatomical features such as surface morphology, wall thickness, unicellular/multicellular structure, and cell type (58, 61). Some of the more advanced trichome specializations include the non-glandular, hooked forms of Loasaceae which entrap potential herbivores (62), or those with a completely cutinized wall as a xerophitic adaptation to prevent evapotranspiration and excessive solar radiation (63). In addition, trichomes can provide a variety of mechanical and/or chemical defense functions against herbivores or pathogens (64). Mature, non-glandular trichomes are composed of a thick cell wall and cuticle layer along with cytoplasmic content that usually disintegrates (23, 60). Despite being physiologically ‘dead’, the trichome function persists (61). The cell wall of non-glandular trichomes tends to be thick so as to protect any internal structures, and is also often composed of lignin, cutin, or suberin (22, 61). Accordingly, trichomes preserve well in the fossil record, particularly as inclusions in amber, owing to their thick cuticles with chemical stability and resistance to biological degradation (65, 66).

The most abundant and frequently reported fossil trichomes are the ‘stellate hairs’ from oaks (Fagaceae) and so characteristic of the mid-Eocene Baltic amber (52). Stellate trichomes have also been reported from Mexican amber (Early Miocene), and along with those from the Baltic deposits have been characterized using confocal laser microscopy (67). Cretaceous amber trichomes have been scarcely studied. Branched, non-dendritic trichomes have been discovered in mid-Cretaceous Ethiopian amber and likely originating from ferns of the families Cyatheaceae and Hymenophyllaceae (68). Although the occurrence of trichomes has been reported in Cretaceous ambers from New Jersey, Myanmar, and Spain, they lack further characterization (69–71).

Morphological variability. (For the basic description of the trichomes composing the larval trash packet refer to the main text). Overall, two basic morphologies of trichomes composing the larval trash packet were evident, in part due to different maturation degrees (Fig. S3*A*). The first, type I, has a straight axis and the OSAs are close together, sometimes even in contact, while secondary branches emerge perpendicularly from the axis (Fig. S3*A*, *B*). In type II trichomes, much more abundant than type I, the axis is flexuose (i.e., zigzagged) and the OSAs tend to be well separated, with secondary branches arising at an angle of 70–120º relative to the main axis and always directed apically away from the blunt base or trichome insertion (Figs. 3*B* and S3*A*, *C*).

When comparing individual trichomes, the length of the trichome base (length between the blunt base of the axis and the first secondary branch) is relatively similar, ranging from 20 to 30 μm, while the axis' total length is understandably more variable, ranging from 140 to 550 μm, but normally is ca. 300 μm long. Length of an individual secondary branch is similarly quite variable, with some extending more than a millimeter in total length (2,200 μm the longest measured). A few long remains present in the trash packet could correspond to extremely long secondary branches from old, highly differentiated trichomes.

We recognized very similar trichome morphologies when examining several isolated trichomes from the Peñacerrada I outcrop (sample MCNA 10023, Fig. S3*F*, *G*), and one trichome adhered to the leg of an oonopid spider, *Orchestina* sp., from the San Just Outcrop (sample CPT 4100) (72). Furthermore, we have recognized in the bibliography very similar trichome morphologies in Late Albian Burmese amber (2).

Trichome identity. The morphology of the fossil trichomes is compared to those in extant plants in order to identify them. For that comparison, all the plant groups that could produce trichomes and are present in the El Soplao outcrop were first considered. The plant meso- and macroremains (cuticles) from El Soplao belong to extinct conifers (cheirolepidiaceans and miroviaceans) and ginkgoaleans (33, 36). These lineages are also recognizable in the palynological record, along with other conifers (araucariaceans, cupressaceans/taxodiaceans, and pinaceans) and other vascular plants, such as leptosporangiate ferns, pteridospermophytes (caytonialeans and peltaspermaleans), and even early flowering plants (magnoliids and monocots) (33).

Among the leptosporangiate ferns, palynological evidence from the El Soplao outcrop demonstrates the presence of Cyathaceae/Dicksoniaceae, Gleicheniaceae, Schizaeaceae, Marsilaceae, and Osmundaceae (33). Among these, the presence of multiseriate and even dendritic trichomes is well-known for gleicheniaceans (73, 74), a lineage widespread during the Early Cretaceous (75–77). *Gleichenia chaloneri* Herendeen & Skog, 1998, an Albian species from England preserved as fusainized remains shows dendritic trichomes associated with pinnules and sori (80), similar in shape and size to those recovered from El Soplao. Gleicheniaceae are known from El Soplao such as the spore species *Gleicheniidites senonicus* Ross, 1949 (33) and *Ornamentifera peregrina* (Bolchovitina, 1953) Bolchovitina, 1968 (Fig. S4).

In the gymnosperm lineages present in El Soplao, trichomes are either uncommon or non-dendritic. Among Cheirolepidaceae the trichomes are principally found associated with

cones, microsporophylls, and free leaves, and, when known, are conical and non-branched (79–83). In addition, though cycads exhibit a dense wool of very long trichomes covering the base of young leaves and cataphylls (i.e., ramentum), these are also non-branched (84). Trichomes in Cretaceous magnoliids have non-branched morphologies which are associated to inflorescences (85–88). Moreover, although there is evidence of dendritic trichomes in different groups of modern monocots, they are primarily restricted to inflorescences (89, 90), less available than leaf trichomes in terms of time and abundance for being potentially harvested by trash-carring larvae. The possibility that the trichomes would have belonged to an eudicot, though less plausible as its presence has not been evidentiated in El Soplao, should not be discarded. Among the basal eudicots, which radiated during the Early Cretaceous (91), dendritic trichomes can be found within the Platanaceae (92). Interestingly, there has been documented an extant chrysopid larva (*Ceraeochrysa lineaticornis*) that incorporates stellate trichomes to its trash packet exclusively gathered from *Platanus wrightii* leaves (Platanaceae) (16). Within rosids and asterids, the two main clades of the eudicots that radiated during the Late Cretaceous (91), dendritic trichomes are nowadays extremely diverse and can be widely found among very different groups (58, 60). In fact, dendritic trichomes with a flexuose main axis, thus with a high resemblance to those composing the trash packet from El Soplao's larva, have been noted in the recent asterid families Lamiaceae and Acanthaceae (93–95). However, asterids have their first known occurrence in the Turonian of New Jersey (96, 97), and only molecular studies hypothesize their origin back to the Early Cretaceous (98, 99). In conclusion, apart from the gleicheniacean ferns, the remaining plant families known from El Soplao seem were not the sources of the trichomes harvested by *Hallucinochrysa diogenesi*.

Paleoecological implications. Ecological studies have demonstrated that gleicheniacean ferns are primary succession pioneers, following wildfires or lava flows (24, 100, 101). Indeed, the gleicheniacean fossil record is well represented by charcoalified and fusainized remains, indicating that they were present as colonizers in fire-prone environments, at least, since the Late Jurassic (78, 102, 103). Charcoal or fusinite are not only copiously present in the Spanish amber-bearing levels, but also sometimes found as inclusions within amber (25, 33). Given the abundance of the amber deposits and their pervasiveness in the Albian outcrops of Spain (25), it seems evident that wildfires were a prominent feature of the forest functioning, promoting both resin production and subsequent erosion of partially burnt litter where the detached resin was primarily buried (33), and permitting the perpetual invasion of primary succession lineages such as Gleicheniaceae. The plant-insect relationship presented in this paper represents possible paleoecological evidence reinforcing this scenario. Additional evidence is the presence of an anaxyelid woodwasp in Álava amber (104), a group whose extant representatives lay eggs in burnt coniferous trees shortly after wildfires, as well as the diversity of snakefly species in Spanish amber, including some preserved with charcoalified plant remains (105).

Trichome autofluorescence. Resistant biomacromolecules can be preserved in the fossil record (106, 107–109). As has been detected from biological remains preserved in amber, some of these biomacromolecules maintain their autofluorescence (35, 67, 110–113). Although amber has its own autofluorescence when excited with UV light, the filters employed permitted us to discriminate the autofluorescence produced by specific trichome biomolecules despite their low

intensity. Autofluorescence of the trash packet trichomes was only detected with UV excitation (Ex/Em: 365/420-470 nm), although the blue emission recorded was mainly localized on the micropapillae on the wall's surface (Fig. 3*G*). Autofluorescence was also detected on the walls of germane trichomes found in other Spanish ambers, as Peñacerrada I amber (Fig. S3*F*, *G*). This blue autofluorescence in the trichome cuticle indicates the presence of phenols, such as hydroxycinnamic acid and/or flavonoids (114–117). In some modern ferns, such as the genus *Pityrogramma*, flavonoids are known to pass through the cell wall and cuticle, crystallizing on the surface of trichomes, and apparently possess antimicrobial properties against plant pathogens (114).

Geological context

The formation of the Basque-Cantabrian Basin (BCB), northern Spain, along with other Mesozoic basins of the Iberian Plate, is associated with the opening of the northern part of the Atlantic. During the Early Cretaceous, sedimentation of the basin was dominated by sandstones, limestones and marls that were deposited in shallow marine and freshwater environments. During the Lower–Middle Albian, at the end of the rift stage, deltaic and estuarine systems developed and evolved vertically into a deltaic system dominated by a fluvial-deltaic environment with siliciclastic input, represented by the Escucha Formation (118). In general, the amber localities of the BCB are related to paralic environments in the eastern region (Escucha Fm.), or paralic-marine environments in the western region (Las Peñosas Fm.) (25). Spanish Cretaceous amber is principally found in localities distributed in a curvilinear arc from the east to the north along the Iberian Peninsula, which corresponds approximately to the seashore during the Early Cretaceous (119).

Three main amber-bearing outcrops are found in the BCB: Moraza, also named Peñacerrada I, in Burgos Province, and Peñacerrada II in Álava Province, both at the eastern BCB and known together as Álava amber (25, 120); and El Soplao in the Autonomous Community of Cantabria, at the western BCB (36). All these amber-bearing outcrops are Albian in age, despite the first and second cited were formerly dated as Upper Aptian–Lower Albian. Other important Spanish outcrops of Albian age are Arroyo de la Pascueta and San Just in Teruel Province (69, 121, 122). All these deposits originated in deltaic environments and contain abundant, exceptionally well preserved plant cuticles.

The El Soplao amber-bearing deposit is geographically localized near the municipality of Rábago (Cantabria). Stratigraphically, it occurs in the Las Peñosas Fm., a non-marine to transitional marine siliciclastic unit that is interleaved within a regressive-transgressive, carbonate-dominated marine sequence of Lower Aptian–Upper Albian age; Las Peñosas Fm. corresponds to the regressive stage of that sequence during the Lower Albian (25, 36). Strata of the El Soplao outcrop are located in a unit of heterolithic sandstones-siltstones and carbonaceous mudstones related to broadly coastal delta-estuarine environments (36). A level of organich-rich clays, 0.7 to 2.5 m thick, contains the amber pieces together with dinoflagellates, spores of vascular cryptogames, pollen grains of gymnosperms and angiosperms, abundant gymnosperm plant cuticle remains, fusainized wood, and marine or brackish-water invertebrates as gastropods and bivalves. Serpulids and bryozoans encrusting some amber surfaces have been

also found (33). The taphonomic data indicates that the amber had a parautochtonous origin in which paleofires promoted both resin production and erosion of the litter containing resin pieces (26, 33). Up to now, this amber has yielded more than five hundred arthropod bioinclusions belonging to arachnids (acari and spiders) and insects of 11 recognized orders: Blattaria, Isoptera, Psocoptera, Thysanoptera, Raphidioptera, Neuroptera, Hemiptera, Coleoptera, Trichoptera, Hymenoptera, and Diptera. Stalactite-shaped amber pieces, very rich in bioinclusions due to their aerial origin (108), are especially abundant in the outcrop, as well as amber pieces with a very characteristic blue-violet fluorescence (34, 36).

Data used in Figure 4

Abbreviations. FEC: Fossil evidence of camouflage. FR: Fossil range. The ranges shown in the figure for those categories that contain more than one family correspond to the family written in italics here. The oldest records and group ranges are calibrated by geochronology (123).

ECHINODERMS (Phylum ECHINODERMATA). Sea urchins (Cl. Echinoidea). Attach stones, and animal and plant debris to their body using their ambulacral podia (124–126). FEC: absent. FR: Ordovician – Recent (127).

GASTROPODS (Phylum MOLLUSCA, Cl. Gastropoda). Euomphalid gastropods (F. †Euomphalidae). Agglutinated exoskeletons to their shell presumably with mucous secretion (128). FEC: Early Devonian (129). FR: Early Devonian (Late Cambrian?) – Late Permian (130). **Xenophorid gastropods** (Clade Littorinimorpha: F. Xenophoridae). Agglutinate exoskeletons, stones, and sand grains to their shell with mucous secretion (131). FEC: Cenomanian (Late Cretaceous); Eocene; Oligocene; Early Miocene (129). FR: Late Cretaceous – Recent (131, 132). **Scaliolid and turritellid gastropods** (Clade Sorbeoconcha: SupF. Cerithioidea: F. Scaliolidae, *Turritellidae*). Agglutinate sand grains and other debris to their shell with mucous secretion (133, 134). FEC: Eocene (Scaliolidae); Late Miocene (Turritellidae) (134, 135). FR: Early Cretaceous – Recent (Turritellidae); Late Cretaceous – Recent (Scaliolidae) (132, 134). **Enid gastropods** (Clade Stylommatophora: F. Enidae). Agglutinate soil or lichens to their shell with mucous secretion (136, 137). FEC: absent. FR: Eocene – Recent (138).

ARTHROPODS (Phylum ARTHROPODA). Sand-covering spiders (Cl. Arachnida: O. Araneae: F. Paratropididae, Microstigmatidae, Pisauridae, *Sicariidae*, Homalonychidae, Zodariidae). Attach sand grains to specialized body setae (138, 140). FEC: absent. FR: Eocene – Recent (Pisauridae, Zodariidae); Miocene – Recent (Microstigmatidae, Sicariidae); no fossil record (Paratropididae, Homalonychidae) (141). **Decorating crabs** (Cl. Malacostraca: O. Decapoda: F. Dromiidae, Dorippidae, *Homolidae*, Xanthidae, and families within the superfamily Majoidea). Attach animal and plant debris, stones, or living organims to hooked body setae or specialized pereiopods (142–145). FEC: absent. FR: Late Jurassic – Recent (Homolidae); Late Cretaceous – Recent (Dorippidae); Paleocene (inferred appearance in the Jurassic) – Recent (Dromiidae); Early Eocene (inferred appearance in the Cretaceous) – Recent (Majoidea); Late Eocene – Recent (Xanthidae) (146).

INSECTS (camouflage only in immature stages) (Cl. Insecta). Assassin bugs (O. Hemiptera: F. Reduviidae). Attach animal and vegetal debris to glandular or mechanically

specialized body setae (147). FEC: Early Miocene, Dominican and Mexican amber (129, 148). FR: Early Cretaceous – Recent (2). **Barklice** (O. Psocoptera: F. Psocidae, Troctopsocidae). Attach debris (and their own faeces) with silk to glandular body setae (149, 150). FEC: Early Miocene, Dominican amber (129). FR: Late Jurassic – Recent (2).

Neuropterans (O. Neuroptera): Attach animal and vegetal debris to specialized body setae and setose tubercles (13, 151, 152). **Owlflies** (F. Ascalaphidae). FEC: Early Miocene, Dominican amber (8). FR: Eocene (inferred appearance around limit Jurassic – Cretaceous) – Recent (2). **Split-footed lacewings** (F. Nymphidae). FEC: absent. FR: Jurassic – Recent (2). **Green lacewings** (F. Chrysopidae and extinct allies, i.e. superfamily Chrysopoidea). FEC: Albian, Spanish amber; Middle Eocene, Baltic amber (49). FR: see below.

Case-building insects (marked with asterisks): Leaf beetles (O. Coleoptera: F. Chrysomelidae). Build a case with their own faeces, incorporating plant debris, using salivary secretions (153). FEC: Middle Eocene, Baltic amber; Early Miocene, Dominican amber (154). FR: Late Cretaceous – Recent (2). **Tineiod moths** (O. Lepidoptera: F. Tineidae, Psychidae). Build a case with their own faeces, incorporating plant debris, using silk (155). FEC: Middle Eocene, Baltic amber; Early Miocene, Dominican amber (2, 129). FR: Eocene (inferred appearance in the Cretaceous) – Recent (2). **Caddisflies** (O. Trichoptera). Build a case with sand grains or animal and plant debris using silk (156). FEC: very common in the fossil record, known since the Early Jurassic (2, 157). FR: Early Triassic – Recent (2).

Other invertebrates cover themselves with exogenous elements. Sea anemones and polychaetes actively select exogenous elements and attach them to their body structures (column and tube, respectively) but without proven camouflaging implications (158–160). Moreover, phoronids and sand-cementing bivalves agglutinate exogenous elements to their body structures (tube and shell, respectively) but passively (161–164).

Figure box. Spanish amber: *Hallucinochrysa diogenesi* gen. et sp. nov., oldest trash-carrying behavior and trumpet-shaped empodia (this report). **Canadian amber**: stalked eggs (27). **Baltic amber**: figured green lacewing larva carrying a trash packet of ‘stellate hairs’ (oak trichomes) and other plant remains (49), and lost specimen of a larva with some trichomes in the vicinity as possible remains of a trash packet, which was described originally as Hemerobiidae but possible belonging to Chrysopidae according to a subsequent interpretation (50, 51). **Dominican amber**: complete larva with trumpet-shaped empodia and setigerous tubercles but without evidences of trash packet (8).

The localities where adult Chrysopoidea have been described are as follows: the Early Jurassic of Luxembourg, the Late Jurassic of Germany, Kazakhstan, and China, the Early Cretaceous of Brazil, Spain, Russia, Mongolia, and China, the Late Cretaceous of Russia, the Paleocene/Eocene of Denmark, the Late Eocene of France, the Late Eocene of England, the Eocene and Late Eocene/Early Oligocene of USA, the Oligocene of Germany, the Late Oligocene of France, the Early Miocene of Spain, the Miocene of Hungary, and the Middle Miocene of Russia (7). The trumpet-shaped empodia can be considered an adaptation to capture and retain active prey due to an efficient anchoring to the substrate (57).

Supporting References

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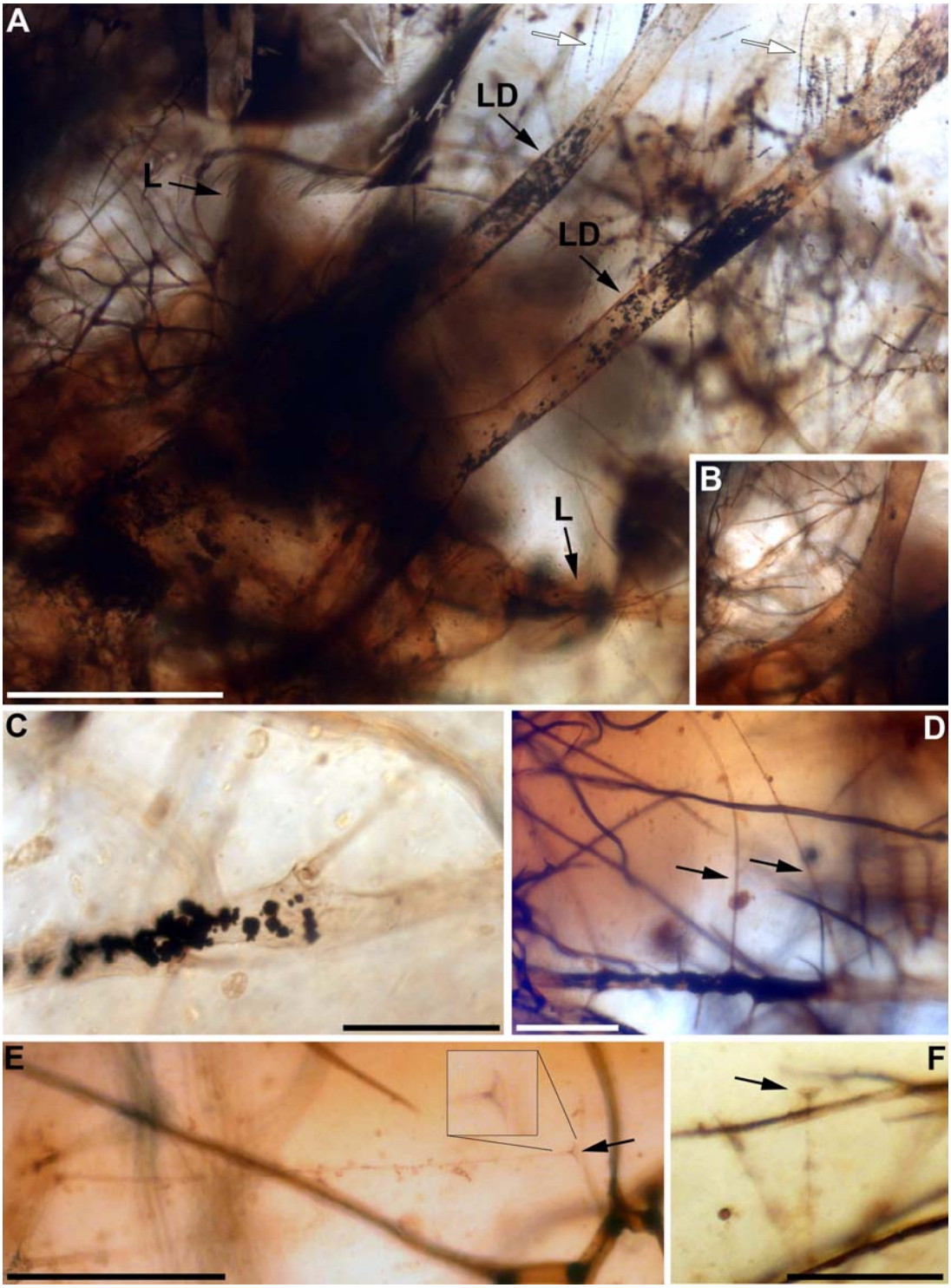
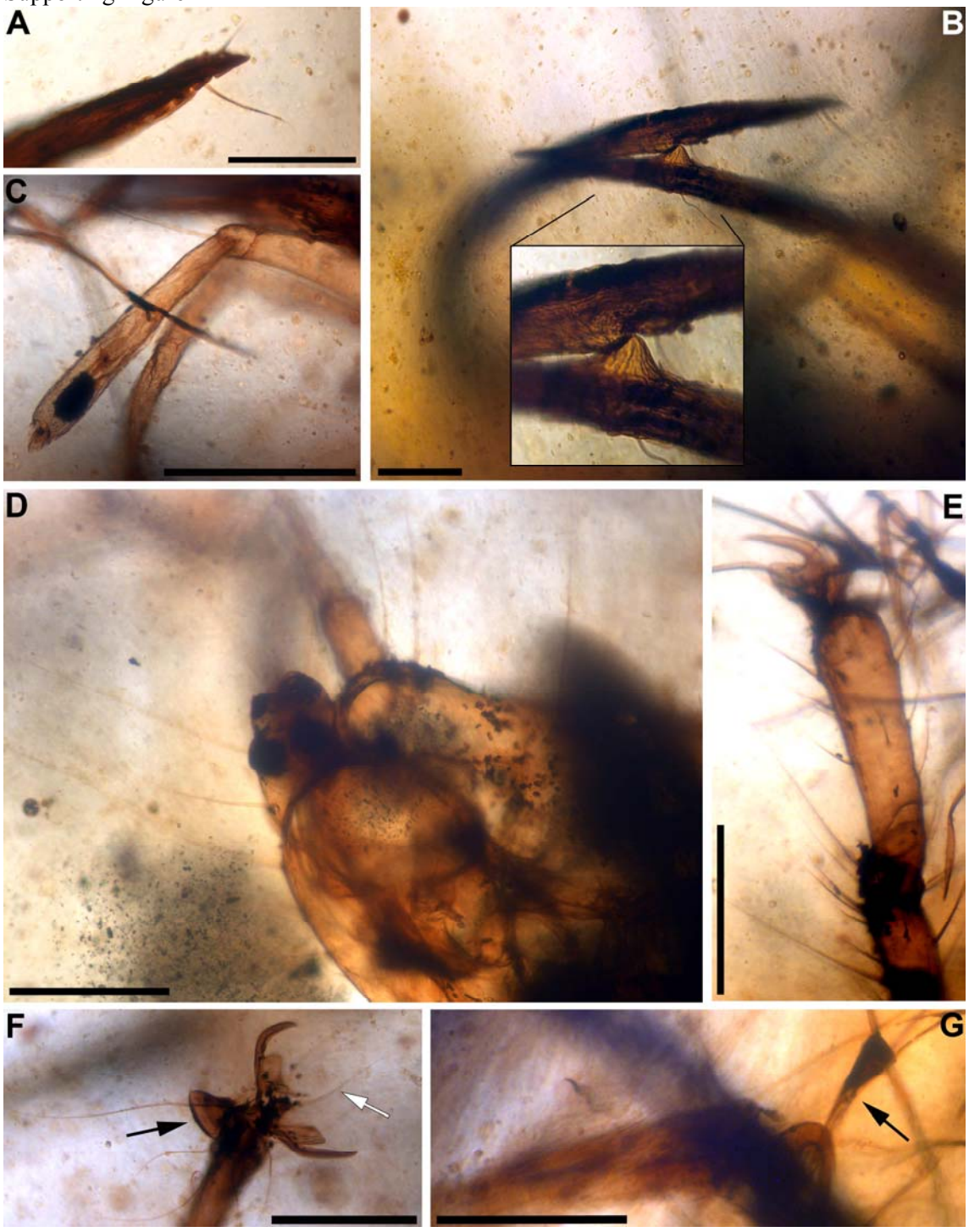
Supporting Figure 1



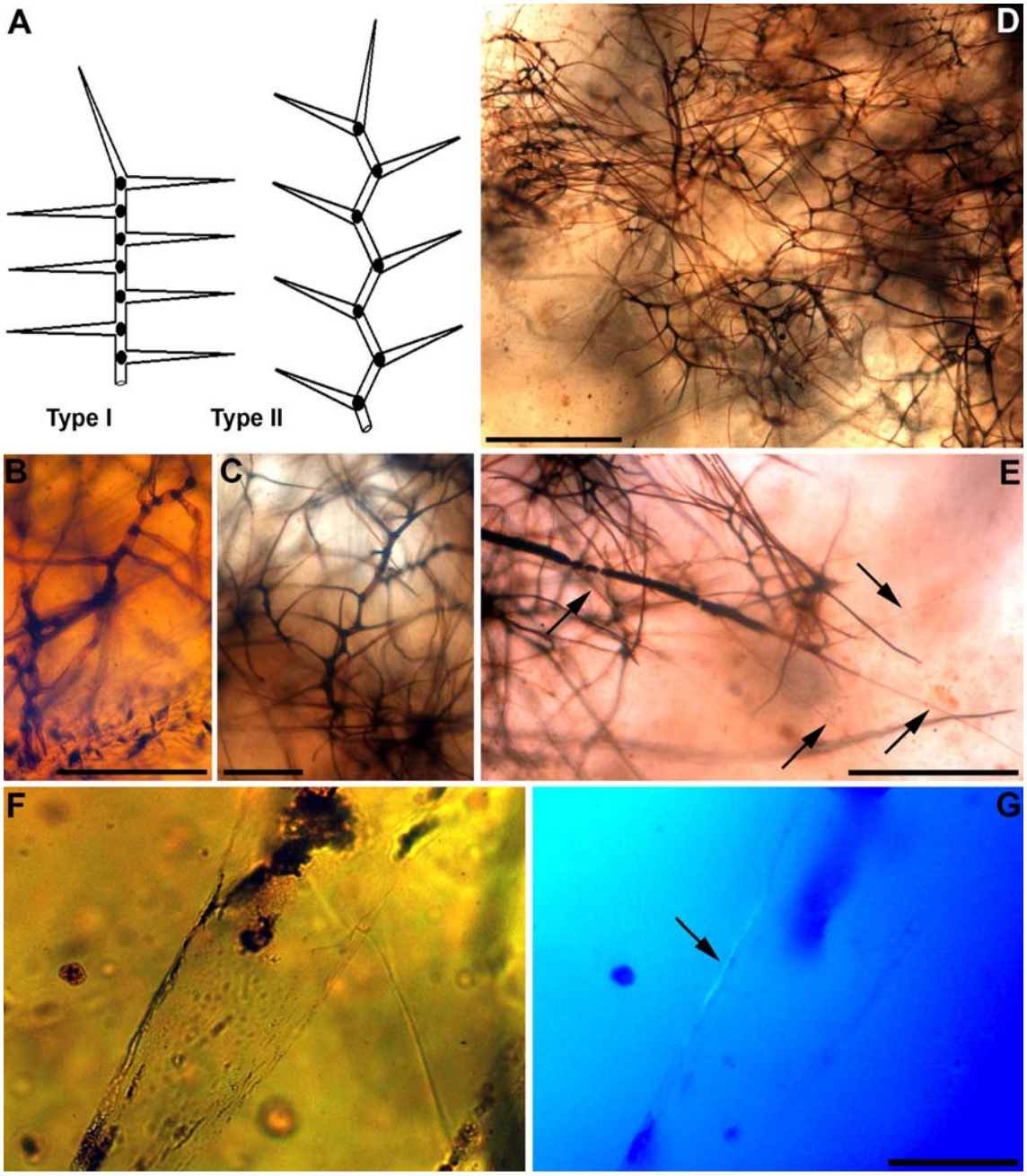
Tubular tubercles of *Hallucinochrysa diogenesi* gen. et sp. nov. (*A*) Lateral (L) and laterodorsal (LD) pairs of prothoracic tubular tubercles in dorsal view; laterodorsal pair showing some sub-basal setae (white arrows). (*B*) Insertion of the left prothoracic lateral tubular tubercle (same scale as in *A*). (*C*) Apex of an abdominal tubular tubercle showing a setal insertion and pyrite crystals (black deposits). (*D*) Right metathoracic lateral tubular tubercle showing curved setae (arrows), and pyrite crusts in some parts of the tubular tubercle (black portions). (*E*) Erect seta emerging from a thoracic tubular tubercle, showing its trumpet-shaped ending (arrow), magnified at the inset. (*F*) Trumpet-shaped ending (arrow) of another tubular tubercle seta. Scale bars = (*A*) 0.5 mm, (*C*) 0.05 mm, (*D*, *E*) 0.2 mm, (*F*) 0.1 mm.

Supporting Figure 2



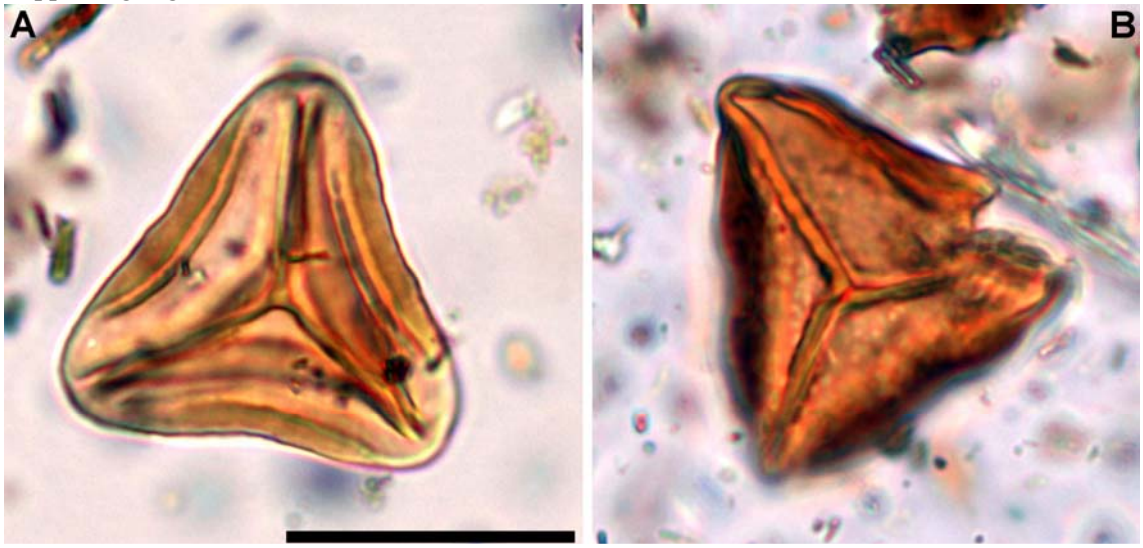
Anatomical head and leg details of *Hallucinochrysa diogenesi* gen. et sp. nov. (*A*) Apex of the right jaw showing serration on inner margin and distal sensilla. (*B*) Coupling system at jaw apices, with inset showing a magnification of this structure. (*C*) Terminal left labial palpomere, showing a distal conical papilla. (*D*) Head in ventral view showing prominent ocular tubercle with four stemmata, antennal pedicel, and long setae emerging from grooves. (*E*) Right prothoracic tarsus showing pretarsal claws in lateral view. (*F*) Left prothoracic pretarsal claws in ventro-oblique view with conspicuous basal expansions, fine pulvilli (white arrow pointing to the left pulvillus) and distal pad of the trumpet-shaped empodium, distorted by preservation (black arrow). (*G*) Left metathoracic tarsus showing part of a pretarsal claw in lateral view and the trumpet-shaped empodium (arrow). Scale bars = (*A*, *B*) 0.1 mm, (*C*–*G*) 0.2 mm.

Supporting Figure 3



Further morphological features of the trichomes of gleicheniacean fern affinity from the trash packet of *Hallucinochrysa diogenesi* and autofluorescence of a germane trichome from Álava amber (MCNA 10023). (*A*) Two types of trichomes outlined within text. (*B*) Trichomes type I. (*C*) Trichome type II. (*D*) Detail of the trash packet showing abundant trichomes. (*E*) Several trichomes entangled among setae (arrows) of an abdominal tubular tubercle. (*F*) Detail of a trichome branch from Álava amber, at same scale that *G*. (*G*) Same detail that (*F*) under fluorescence microscopy (arrow indicates autofluorescence signal). Scale bars = (*B*, *C*) 200 μm, (*D*, *E*) 500 μm, (*G*) 25 μm.

Supporting Figure 4



Fern spores of gleicheniacean fern affinity from the amber-bearing sediments of the El Soplao outcrop. (*A*) *Gleicheniidites senonicus*. (*B*) *Ornamentifera peregrina*. Scale bar = 20 μm (both subfigures at same scale).

Movie Legends

Movie S1. Morphological and locomotive reconstruction of *Hallucinochrysa diogenesi.*

Movie S2. Micropapillae from a trichome within the trash packet of *Hallucinochrysa diogenesi* under fluorescence microscopy.

ANEXO II. Listado de inclusiones de artrópodos de El Soplao

Las entradas correspondientes a ejemplares de la serie tipo (holotipos o alotipos), ejemplares figurados o referenciados en publicaciones, o nuevos géneros y/o especies han sido resaltados en negrita. Los holotipos o alotipos han sido marcados en rojo, mientras que los figurados o referenciados en publicaciones se han resaltado en azul.

Abreviaciones del campo "Clase"

A - Arachnida, E - Enthognata, I - Insecta, M - Malacostraca, R - "Reptilia"

Abreviaciones del campo "Estatus"

A - Alotipo, F - Figurado, H - Holotipo, R - Referenciado

RS - Referencia de Sininclusión (véase el apartado 3.2.4)

CES		Clase	Orden (y otros rangos taxonómicos)	Familia	Género	Especie	Estatus	RS
001		I	Hymenoptera: Platygastroidea	Platygastridae				01
002		I	Thysanoptera					01
003		I	Hymenoptera: Platygastroidea	Platygastridae				01
004		**I**	**Neuroptera: Hemerobiiformia: Mantispoidea**	**Berothidae**	**NUEVO GENERO**	**NUEVA ESPECIE**		01
005		I	Diptera: Brachycera					01
006		I	Hymenoptera: Platygastroidea	Platygastridae				01
007		I	Diptera					02
008		**I**	**Diptera: "Nematocera": Culicomorpha**	**Ceratopogonidae**	***Austroconops***		**R**	02
009		I	Hymenoptera: Platygastroidea	Platygastridae				24
010	.1	I	Hemiptera: Heteroptera					24
	.2	I	Hemiptera: Heteroptera					
	.3	I	Hemiptera: Heteroptera					
011		I	Hymenoptera: Platygastroidea	Platygastridae		**NUEVA ESPECIE**		24

012		I	Thysanoptera					24
013	**.1**	**A**	**Araneae: Dysderoidea**	**Oonopidae**	***Orchestina***	***O. rabagensis***	**H**	07 (25, 26)
	.2	I	Hymenoptera: Platygastroidea	Platygastridae				
014		I	Neuroptera: Hemerobiiformia: Mantispoidea	Berothidae	*Ethiroberotha?*			07 (25, 26)
015	.1	I	Neuroptera: Hemerobiiformia: Coniopterygoidea	Coniopterygidae	*Glaesoconis*			07 (25, 26)
	.2	**I**	**Diptera: Brachycera**	**Zhangsolvidae**	**NUEVO GENERO**	**NUEVA ESPECIE**		
	.3	**I**	**Diptera: Brachycera**	**Zhangsolvidae**	**NUEVO GENERO**	**NUEVA ESPECIE**		
	.4	I	Hymenoptera: Platygastroidea	Platygastridae				
	.5	**I**	**Diptera: Brachycera**			**NUEVA ESPECIE A**		
016	.1	A	Araneae: Araneoidea	Araneidae?				07 (25, 26)
	.2	**I**	**Diptera: Brachycera**			**NUEVA ESPECIE A**		
017	**.1**	**I**	**Diptera: "Nematocera": Culicomorpha**	**Ceratopogonidae**	***Austroconops***		**F**	
	.2	I	Hymenoptera: Platygastroidea	Platygastridae				
	.3	I	Hymenoptera: Platygastroidea	Platygastridae				
	.4	I	Hymenoptera: Platygastroidea	Platygastridae				
018	.1	I	Hymenoptera	Maimetshidae				
	.2	I	Hymenoptera	Maimetshidae				
	.3	I	Hymenoptera	Maimetshidae				
	.4	I	Hymenoptera: Aculeata: Chrysidoidea					
	.5	I	Hymenoptera					
019	.1	A	Araneae					
	.2	I	Coleoptera					
054		I	Hymenoptera: Platygastroidea	Platygastridae				
055		I	Hemiptera: Auchenorrhyncha: Fulgoroidea					
056	.1	I	Hymenoptera: Platygastroidea	Platygastridae				
	.2	I	Hymenoptera: Platygastroidea	Platygastridae				
	.3	I	"Blattaria"					
057	.1	I	Coleoptera: Polyphaga: Elateriformia: Elateroidea					
	.2	I	Coleoptera					
	.3	I	Psocodea: Psocoptera					

	.4	A	Araneae					
	.5	I	Hymenoptera: Platygastroidea	Platygastridae				
	.6	I	Hymenoptera: Platygastroidea	Platygastridae				
	.7	I	Hymenoptera: Platygastroidea	Platygastridae				
058	.1	I	Hymenoptera: Aculeata: Chrysidoidea					
	.2	I	Hymenoptera: Platygastroidea	Platygastridae				
	.3	I	Diptera					
059	.1	I	Diptera: "Nematocera"					
	.2	I	Hymenoptera					
	.3	I	Coleoptera: Polyphaga: Staphyliniformia: Staphylinoidea	Staphylinidae				
060	1	I	Homoptera: Sternorrhyncha	Aleyrodidae				
	2	I	Hymenoptera: Platygastroidea	Platygastridae				
130	.1	I	Hymenoptera: Platygastroidea	Platygastridae				
	.2	I	Hymenoptera: Platygastroidea	Platygastridae				
	.3	I	Hymenoptera: Platygastroidea	Platygastridae				
	.4	I	Hymenoptera: Platygastroidea	Platygastridae				
	.5	I	Hymenoptera: Aculeata: Vespoidea	Tiphiidae?				
	.6	I	Hymenoptera: Aculeata: Vespoidea	Tiphiidae?				
	.7	I	Hymenoptera					
	.8	I	"Blattaria"					
315	.1	I	Coleoptera					
	.2	I	Diptera: "Nematocera"					
	.3	I	Hymenoptera: Serphitoidea	Serphitidae				
	.4	I	Diptera: "Nematocera"					
	.5	I	Hymenoptera: Platygastroidea	Platygastridae				
	.6	I	Diptera: "Nematocera": Culicomorpha	Chironomidae				
	.7	I	Diptera					
	.8	I	Psocodea: Psocoptera					
316	.1	I	Hymenoptera					
	.2	A	Araneae					
	.3	I	Hymenoptera					
	.4	I	Diptera Brachycera					

	.5	I	Diptera					
	.6	I	Hymenoptera: Aculeata: Vespoidea	Tiphiidae?				
	.7	I	Lepidoptera					
	.8	I	Hymenoptera					
	.9	I	Diptera					
	.10	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae	*Lebanoculicoides?*			
	.11	I	Diptera					
	.12	I	Hymenoptera					
	.13	I	Hymenoptera					
	.14	I	Hymenoptera					
	.15	I	Lepidoptera					
	.16	I	Diptera: "Nematocera"					
	.17	I	Diptera: "Nematocera"					
	.18	I	Diptera					
332		I	Hymenoptera					
348		**I**	**Neuroptera: Hemerobiiformia: Coniopterygoidea**	**Coniopterygidae**	***Glaesoconis***	**NUEVA ESPECIE**		26 (07, 25)
349	**.1**	**I**	**Diptera: Brachycera: Stratiomyomorpha**	**Zhangsolvidae**	**NUEVO GENERO**	**NUEVA ESPECIE**		26 (07, 25)
	.2	**I**	**Diptera: Brachycera**			**NUEVA ESPECIE A**		
350	.1	I	Psocodea: Psocoptera					26 (07, 25)
	.2	I	Hymenoptera					
351		I	Homoptera: Sternorrhyncha: Psylloidea					26 (07, 25)
352	**.1**	**I**	**Diptera: Brachycera: Eremoneura**	**Chimeromyiidae**	***Chimeromyia***	**NUEVA ESPECIE**		26 (07, 25)
	.2	I	Hemiptera?					
	.3	**I**	**Diptera: Brachycera**			**NUEVA ESPECIE B**		
	.4	I	Neuroptera: Hemerobiiformia: Coniopterygoidea	Coniopterygidae				
353	**.1**	**I**	**Diptera: Brachycera**			**NUEVA ESPECIE B**		26 (07, 25)
	.2	I	Hymenoptera: Platygastroidea	Platygastridae				
354		**I**	**Diptera: Brachycera**			**NUEVA ESPECIE B**		26 (07, 25)
355		I	Hymenoptera: Serphitoidea	Alavarommatidae?				26 (07, 25)
356		I	Hymenoptera: Platygastroidea	Platygastridae				26 (07, 25)
357		Indet.						26

								(07, 25)
358		I	Diptera: "Nematocera": Culicomorpha	Chironomidae				
359		I	Diptera: "Nematocera": Psychodomorpha	Psychodidae: Phlebotominae	*Eophlebotomus*			
360		I	Diptera: Brachycera: Tabanomorpha	Rhagionidae	*Litoleptis*			
361		I	Coleoptera: Polyphaga: Cucujiformia: Cucujoidea	Latridiidae				
362		**A**	**Araneae**	**Lagonomegopidae**	***Soplaogonomegops***	***S. unzuei***	**H**	30
363		**I**	**Diptera: "Nematocera": Culicomorpha**	**Ceratopogonidae**	***Atriculicoides***	***A. szadziewskii***	**H**	
364	**.1**	**I**	**Raphidioptera**	**Mesoraphidiidae**	***Amarantoraphidia***	***A. ventolina***	**H**	
	.2	**I**	**Hymenoptera: Evanioidea**	**Evaniidae**	***Cretevania***	***C. soplaensis***	**H**	
	.3	I	Hymenoptera					
	.4	I	Hymenoptera					
	.5	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
	.6	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
	.7	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
	.8	I	Diptera: Brachycera: Eremoneura	Chimeromyiidae				
	.9	I	Hymenoptera					
	.10	I	Thysanoptera					
365		I	Hymenoptera: Serphitoidea					23
366		A	Acari: Acariformes: Trombidiformes	Bdellidae	*Spinibdella?*			23
367		I	Thysanoptera					23
368		I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae	*Austroconops?*			
369		**A**	**Araneae**				**F**	
370		I	Hymenoptera					19
371		A	Acari: Acariformes: Oribatida					19
372		I	Diptera: Brachycera: Eremoneura: Empidoidea	Hybotidae	*Trichinites*			
374		I	Hymenoptera					22
375		I	Hymenoptera: Apocrita					22
376		I	Raphidioptera	Mesoraphidiidae				21
377	.1	I	Diptera: "Nematocera": Culicomorpha	Chironomidae				21

	.2	I	Hymenoptera: Platygastroidea	Platygastridae				
	.3	I	Hymenoptera					
378		Indet.						18
379		I	Diptera: Brachycera: Eremoneura: Empidoidea	Atelestidae	*~Nemedina*			
380		M	Tanaidacea					
381		I	Hymenoptera					18
382	.1	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
	.2	I	Hymenoptera					
383		I	Hymenoptera: Evanioidea	Aulacidae?/ Gasteruptiidae?				
384		I	Hymenoptera: Aculeata: Chrysidoidea	Bethylidae				
385		I	Hymenoptera: Aculeata: Vespoidea					23
386	.1	I	Hymenoptera	Maimetshidae				23
	.2	I	Diptera					
	.3	I	Hemiptera					
387		I	Hymenoptera: Platygastroidea	Platygastridae				23
388		I	Hymenoptera					
389	.1	A	Araneae					
	.2	I	Hymenoptera					
	.3	I	Diptera: Brachycera: Eremoneura: Empidoidea	Dolichopodidae	*Microphorites?*			
	.4	A	Araneae					
	.5	A	Acari: Acariformes: Trombidiformes	Erythraeidae	*Leptus*			
	.6	I	Hymenoptera: Platygastroidea	Platygastridae				
390	**.1**	**I**	**Neuroptera: Myrmeleontiformia: Nemopteroidea**	**Psychopsidae**	**NUEVO GENERO**	**NUEVA ESPECIE**		25 (07, 26)
	.2	A	Araneae					
	.3	**I**	**Diptera: Brachycera**			**NUEVA ESPECIE A**		
	.4	A	Acari					
	.5	I	Hymenoptera: Platygastroidea	Platygastridae				
391	**.1**	**I**	**Raphidioptera**	**Mesoraphidiidae**	***Necroraphidia***	***N. arcuata***	**H**	25 (07, 26)
	.2	**I**	**Hymenoptera: Megalyroidea**	**Megalyridae**	***Megalava***	***M. truncata***	**F**	
	.3	I	Coleoptera					
	.4	I	Coleoptera					
	.5	I	Hymenoptera: Serphitoidea	Mymarommatidae				
	.6	I	Hemiptera: Sternorrhyncha					
392	.1	I	Lepidoptera	Micropterigidae				25

	.2	**I**	**Diptera: Brachycera: Stratiomyomorpha**	**Zhangsolvidae**	**NUEVO GENERO**	**NUEVA ESPECIE**		(07, 26)
	.3	**I**	**Diptera: Brachycera: Stratiomyomorpha**	**Zhangsolvidae**	**NUEVO GENERO**	**NUEVA ESPECIE**		
	.4	I	Neuroptera: Hemerobiiformia: Coniopterygoidea	Coniopterygidae				
	.5	I	Hymenoptera: Platygastroidea	Platygastridae				
	.6	A	Acari					
	.7	**I**	**Diptera: Brachycera**			**NUEVA ESPECIE A**		
	.8	A	Araneae					
	.9	I	Hymenoptera					
393		I	Hymenoptera: Platygastroidea	Platygastridae				
394		I	Hymenoptera					
395		I	Hymenoptera: Platygastroidea	Platygastridae				03
396	.1	I	Diptera: Brachycera: Eremoneura: Empidoidea	Dolichopodidae	*Microphorites*			03
	.2	I	Diptera: Brachycera: Eremoneura: Empidoidea	Dolichopodidae	*Microphorites*			
397		I	Hymenoptera	Maimetshidae?				
398		I	Hymenoptera: Ceraphronoidea	Stigmaphronidae				
399		I	Hymenoptera: Platygastroidea	Platygastridae				
400		I	Hymenoptera: Platygastroidea	Platygastridae				
401	.1	I	Hymenoptera: Platygastroidea	Platygastridae				
	.2	I	Hymenoptera: Platygastroidea	Platygastridae				
	.3	I	Hymenoptera: Platygastroidea	Platygastridae				
	.4	I	Hymenoptera: Platygastroidea	Platygastridae				
	.5	I	Hymenoptera: Platygastroidea	Platygastridae				
	.6	I	Diptera: "Nematocera": Psychodomorpha	Psychodidae				
	.7	I	Hymenoptera					
	.8	I	Hymenoptera: Platygastroidea	Platygastridae				
	.9	I	Thysanoptera					
	.10	I	Diptera: "Nematocera"					
	.11	I	Hymenoptera: Platygastroidea	Platygastridae				
	.12	I	Diptera: Brachycera					
	.13	I	Diptera: Brachycera					
402	.1	I	Neuroptera: Hemerobiiformia:	Berothidae?				

			Mantispoidea					
	.2	I	Hymenoptera: Serphitoidea	Mymarommatidae				
	.3	I	Hymenoptera: Ceraphronoidea	Stigmaphronidae				
	.4	I	Hymenoptera: Platygastroidea	Platygastridae				
	.5	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae	*Atriculicoides*			
	.6	I	Hymenoptera: Platygastroidea	Platygastridae				
	.7	I	Psocodea: Psocoptera					
	.8	I	Hymenoptera: Serphitoidea	Serphitidae				
	.9	I	Thysanoptera					
	.10	I	Thysanoptera					
403		I	Raphidioptera?					
404	.1	I	Diptera: Brachycera: Eremoneura: Empidoidea	Hybotidae	*Trichinites*			
	.2	I	Diptera: Brachycera: Eremoneura: Empidoidea	Hybotidae	*Trichinites*			
405		I	Lepidoptera?					17
406		I	Thysanoptera					17
407		I	Lepidoptera					17
408		A	Araneae	Lagonomegopidae	*Lagonomegops?*			17
409		I	Hymenoptera					25 (07, 26)
410	.1	I	Hymenoptera					25 (07, 26)
	.2	I	Hymenoptera					
	.3	I	Hymenoptera					
411		I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae	*Lebanoculicoides*			25 (07, 26)
412		A	Acari: Acariformes: Oribatida	Trhypochthoniidae	*Afronothrus*			25 (07, 26)
413	.1	I	Psocodea: Psocoptera					16
	.2	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae	*Austroconops?*			
	.3	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
	.4	I	Diptera: Brachycera: Eremoneura: Empidoidea	Dolichopodidae	*Microphorites?*			
	.5	I	"Blattaria"					
414		I	Psocodea: Psocoptera					16
415	.1	I	Hymenoptera					
	.2	I	Indet.					

416		I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae	*Protoculicoides*			
417		I	Hymenoptera: Serphitoidea	Serphitidae				
418		**I**	**Neuroptera: Hemerobiiformia: Chrysopoidea**	**Indet.**	**NUEVO GÉNERO**	**NUEVA ESPECIE**		
420	.1	I	Neuroptera					04
	.2	I	Coleoptera					
	.3	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae	*Archiaustroconops*			
	.4	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
	.5	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae	*Lebanoculicoides*			
	.6	I	Psocodea: Psocoptera					
	.7	I	Coleoptera: Polyphaga: Staphyliniformia: Staphylinoidea	Staphylinidae				
	.8	I	Thysanoptera					
	.9	I	Thysanoptera					
	.10	I	Thysanoptera					
	.11	I	Hymenoptera					
	.12	I	Indet.					
421		I	Hymenoptera: Platygastroidea	Platygastridae				04
422		I	Thysanoptera					04
423	.1	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae	*Lebanoculicoides*			04
	.2	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae	*Lebanoculicoides*			
424		I	Hymenoptera					04
425		I	Coleoptera					04
426	.1	"Aves"						
	.2	I	"Blattaria"?					
427		I	Hymenoptera					05
428		I	Hymenoptera					05
429		I	Hemiptera: Sternorrhyncha	Aleyrodidae				05
430		I	Hymenoptera: Ichneumonoidea	Braconidae				05
431		I	Diptera: Brachycera					06
432		I	Coleoptera: Polyphaga: Cucujiformia: Curculionoidea					06
433	.1	I	Coleoptera: Polyphaga:	Staphylinidae				

			Staphyliniformia: Staphylinoidea					
	.2	I	Coleoptera					
434		I	Diptera: Brachycera: Eremoneura: Cyclorrhapha	Phoridae	*Euliphora*			
435	.1	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
	.2	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
436		I	Thysanoptera					
437		I	Mecoptera					
438		I	Diptera: Brachycera: Eremoneura	Chimeromyiidae	*Chimeromyia*			
439		I	Diptera: Brachycera: Eremoneura: Empidoidea	Hybotidae	*Trichinites*			
440		I	Diptera: Brachycera: Eremoneura: Empidoidea	Dolichopodidae	*Microphorites*			
441		I	Hymenoptera					
442		I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae	*Archiaustroconops*			
444		I	Hymenoptera: Platygastroidea	Platygastridae				
445		I	Psocodea: Psocoptera					
446	.1	I	Isoptera?					
	.2	I	Hymenoptera: Platygastroidea	Platygastridae				
447		I	Hymenoptera: Platygastroidea	Platygastridae				
448		I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
449	.1	I	Psocodea: Psocoptera					
	.2	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
450	.1	I	Hymenoptera: Evanioidea	Evaniidae				
	.2	I	Hymenoptera: Chalcidoidea	Mymaridae?				
	.3	I	Hymenoptera					
	.4	I	Hymenoptera: Platygastroidea	Platygastridae				
	.5	I	Hymenoptera					
	.6	I	Hymenoptera					
	.7	I	Hymenoptera					
451		**I**	**Thysanoptera**	**Thripidae**	***Tethysthrips***	***T. hispanicus***	**H**	
452		**I**	**Hymenoptera: Serphitoidea**	**Mymarommatidae**	***Archaeromma***	***A. hispanicum***	**A**	
453		I	Hymenoptera: Platygastroidea	Platygastridae				

454		I	Hymenoptera: Serphitoidea	Mymarommatidae	*Archaeromma*	*A. hispanicum?*		
455		I	Hymenoptera: Platygastroidea	Platygastridae				
457	.1	Aves?						
	.2	I	Hemiptera: Sternorrhyncha					
458		I	Thysanoptera					
459		I	Neuroptera: Hemerobiiformia: Coniopterygoidea	Coniopterygidae	*Glaesoconis*			
460		I	Neuroptera: Hemerobiiformia: Coniopterygoidea	Coniopterygidae				
461		I	Hymenoptera: Platygastroidea	Platygastridae				
462		I	Hymenoptera: Platygastroidea	Platygastridae				
463		I	Coleoptera: Adephaga	Carabidae				
465		I	Psocodea: Psocoptera					
466		I	Hymenoptera: Platygastroidea	Platygastridae				
467		I	Hymenoptera: Platygastroidea	Platygastridae				
468		I	Hymenoptera: Platygastroidea	Platygastridae				
469		I	Hymenoptera: Platygastroidea	Platygastridae?				
470		I	Hymenoptera: Platygastroidea	Platygastridae				
471		I	Hymenoptera					
472		I	Hymenoptera: Platygastroidea	Platygastridae				
473		I	"Blattaria"					
476	.1	A	Araneae: Araneoidea	Araneidae?				
	.2	I	Hymenoptera					
	.3	I	Hymenoptera: Platygastroidea	Platygastridae				
	.4	I	Diptera					
	.5	I	Neuroptera: Hemerobiiformia: Coniopterygoidea	Coniopterygidae				
	.6	I	Raphidioptera?					
477		I	Neuroptera: Myrmeleontiformia: Myrmeleontoidea	Nymphidae?				
487		I	Coleoptera: Polyphaga: Staphyliniformia: Staphylinoidea	Staphylinidae				09
488		I	Coleoptera: Polyphaga: Cucujiformia: Cucujoidea	Latridiidae				09
489		I	Coleoptera: Polyphaha:	Dermestidae				09

			Bostrichiformia: Bostrichoidea					
490		I	Coleoptera: Polyphaga: Cucujiformia: Cucujoidea	Latridiidae				09
491		I	Thysanoptera					09
492		I	Hymenoptera					09
493		I	Hemiptera: Sternorrhyncha					09
494		A	Acari: Acariformes: Trombidiformes?					09
495	.1	I	Hymenoptera					09
	.2	I	Hymenoptera					
	.3	I	Hymenoptera					
	.4	I	Psocodea: Psocoptera					
496		I	Hymenoptera?					09
497		I	Thysanoptera					09
498		I	Thysanoptera					09
499		I	Hymenoptera					09
500	.1	I	Hymenoptera					09
	.2	I	Hymenoptera					
501		I	Hymenoptera					09
502		I	Indet. *(larva)*					09
503		I	Thysanoptera					09
504		I	Hymenoptera: Serphitoidea	Mymarommatidae				09
505		A	Acari: Acariformes: Oribatida	Nothridae				09
506		I	Diptera					09
507	.1	I	Hemiptera: Heteroptera					10
	.2	I	Coleoptera					
508		I	Hymenoptera: Platygastroidea	Platygastridae				10
509	.1	I	Hymenoptera					10
	.2	I	Hymenoptera					
510		I	Hymenoptera: Platygastroidea	Platygastridae				10
511		I	Hymenoptera: Platygastroidea	Platygastridae?				11
512		I	Coleoptera: Polyphaha: Bostrichiformia: Bostrichoidea	Dermestidae				11
513		I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae	*Archiaustroconops*			11
514		I	Indet. *(larva)*					11
515		I	Coleoptera: Adephaga	Carabidae				13
516	.1	I	Hymenoptera					13
	.2	I	Hymenoptera					

517		I	"Blattaria"					14
518		I	Coleoptera: Polyphaga: Cucujiformia: Tenebrionoidea	Scraptiidae				14
519		I	Coleoptera					
520	.1	I	Coleoptera					12
	.2	I	Hymenoptera					
521		I	Coleoptera					
522		I	Coleoptera: Polyphaga: Elateriformia: Elateroidea					
523		I	Diptera: Brachycera: Eremoneura: Empidoidea	Atelestidae	*Nemedromia?*			
524		I	Coleoptera					
525	.1	I	Coleoptera					15
	.2	I	Coleoptera					
	.3	I	Indet.					
	.4	I	Diptera: Brachycera					
526	.1	I	"Blattaria"					
	.2	A	Acari					
	.3	I	Hymenoptera					
	.4	I	Diptera: "Nematocera"					
	.5	I	Psocodea: Psocoptera					
	.6	I	Psocodea: Psocoptera					
	.7	I	Thysanoptera					
527	.1	I	Hymenoptera					
	.2	I	Diptera: "Nematocera": Psychodomorpha	Psychodidae				
528		I	Diptera: Brachycera: Eremoneura: Empidoidea	Atelestidae	*~Nemedina*			15
529	.1	I	Coleoptera					15
	.2	I	Coleoptera					
	.3	I	Diptera: "Nematocera"					
	.4	I	Diptera: Brachycera					
530	.1	I	Diptera: Brachycera: Tabanomorpha	Rhagionidae				27
	.2	I	Coleoptera: Polyphaga: Elateriformia: Elateroidea					
	.3	I	Hemiptera: Sternorrhyncha	Aleyrodidae				
	.4	I	Hymenoptera: Aculeata: Chrysidoidea	Chrysididae?				
	.5	I	Hymenoptera					

	.6	I	Hymenoptera					
	.7	I	Hymenoptera					
	.8	I	Hymenoptera: Platygastroidea	Platygastridae				
	.9	I	Hymenoptera					
	.10	I	Hymenoptera					
	.11	I	Hymenoptera					
	.12	I	Hymenoptera					
	.13	I	Hymenoptera					
	.14	I	Hymenoptera					
	.15	I	Hymenoptera					
	.16	I	Hymenoptera					
	.17	A	Acari: Parasitiformes: Ixodida	Argasidae				
	.18	A	Acari: Acariformes: Trombidiformes	Erythraeidae	*Leptus*			
	.19	E	Collembola					
	.20	I	Diptera: "Nematocera": Psychodomorpha	Psychodidae: Phlebotominae	*Eophlebotomus*			
	.21	I	Diptera: Brachycera: Eremoneura: Empidoidea	Dolichopodidae	*Cretomicrophorus*			
	.22	I	Diptera: Brachycera: Eremoneura: Empidoidea	Dolichopodidae	*Cretomicrophorus*			
	.23	E	Collembola					
	.24	E	Collembola					
531	.1	I	Diptera: "Nematocera": Culicomorpha	Chironomidae				27
	.2	A	Acari					
532	.1	I	Diptera: Brachycera: Eremoneura: Cyclorrhapha	Phoridae	*Euliphora*			28
	.2	I	Diptera: Brachycera: Eremoneura: Cyclorrhapha	Phoridae	*Euliphora*			
	.3	I	Hymenoptera					
	.4	I	Hymenoptera					
533	.1	I	Diptera: Brachycera: Eremoneura: Cyclorrhapha	Phoridae	*Euliphora*			28
	.2	I	Diptera: Brachycera: Eremoneura: Cyclorrhapha	Phoridae	*Euliphora*			
534		I	Hymenoptera					28
535		I	Diptera: Brachycera: Eremoneura: Cyclorrhapha	Phoridae	*Euliphora*			28
536		I	Hymenoptera					28
537		I	Hymenoptera: Platygastroidea	Platygastridae				28
538		I	Diptera: Brachycera:	Phoridae	*Euliphora*			28

			Eremoneura: Cyclorrhapha					
539		I	Diptera: Brachycera					28
540		I	Diptera: Brachycera: Eremoneura: Cyclorrhapha	Phoridae	*Euliphora*			28
541		R						29
542		I	Thysanoptera					29
543		I	Hymenoptera: Platygastroidea	Platygastridae				29
.544	.1	I	Hymenoptera: Platygastroidea	Platygastridae				
	.2	I	Thysanoptera					
545	.1	I	Hemiptera: Sternorrhyncha					
	.2	I	Hemiptera: Sternorrhyncha					
546		I	Hymenoptera: Platygastroidea	Platygastridae				
547	.1	I	Hymenoptera: Platygastroidea	Platygastridae				
	.2	I	Hymenoptera: Platygastroidea	Platygastridae				
551		I	Hymenoptera: Platygastroidea	Platygastridae				
552		I	Isoptera					
553	.1	I	Hymenoptera					
	.2	I	Hymenoptera					
	.3	I	Psocodea: Psocoptera					
	.4	I	Coleoptera					
	.5	I	Psocodea: Psocoptera					
	.6	I	Hymenoptera					
	.7	I	Hymenoptera					
555		I	Hymenoptera: Platygastroidea	Platygastridae				
556	.1	I	Hymenoptera: Platygastroidea	Platygastridae				
	.2	I	Hymenoptera: Platygastroidea	Platygastridae				
557	.1	I	Hymenoptera: Platygastroidea	Platygastridae				
	.2	I	Hymenoptera: Platygastroidea	Platygastridae				
	.3	I	Hymenoptera					
	.4	I	Hymenoptera					
558	.1	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae	*Archiaustroconops*			
	.2	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae	*Archiaustroconops*			
	.3	I	Hymenoptera: Platygastroidea	Platygastridae				
559		I	Hymenoptera: Platygastroidea	Platygastridae				

560		I	Hymenoptera: Platygastroidea	Platygastridae				
561		I	Hymenoptera: Platygastroidea	Platygastridae				
562	.1	I	Diptera: Brachycera: Eremoneura	Chimeromyiidae	*Chimeromyia*			
	.2	I	Diptera: "Nematocera": Culicomorpha	Chironomidae				
	.3	I	Diptera: "Nematocera": Bibionomorpha	Cecidomyiidae	*Eltxo?*			
564		I	Hymenoptera: Platygastroidea	Platygastridae				29
565	.1	I	Hymenoptera: Platygastroidea	Platygastridae				29
	.2	I	Hymenoptera: Platygastroidea	Platygastridae				
566	**.1**	**I**	**Hymenoptera: Serphitoidea**	**Serphitidae**	***Microserphites***	***M. soplaensis***	**H**	
	.2	I	Coleoptera					
567		I	Coleoptera					
568		I	Hymenoptera: Platygastroidea	Platygastridae				
569		I	Hymenoptera: Platygastroidea	Platygastridae				
570	.1	I	Coleoptera: Polyphaga: Cucujiformia: Cleroidea	Cleridae				
	.2	I	Diptera: Brachycera: Eremoneura	Chimeromyiidae				
571	.1	I	Coleoptera					
	.2	A	Araneae					
	.3	I	Hymenoptera: Platygastroidea	Platygastridae				
	.4	I	Hymenoptera: Platygastroidea	Platygastridae				
	.5	I	Hymenoptera: Platygastroidea	Platygastridae				
	.6	I	Hymenoptera: Platygastroidea	Platygastridae				
572		I	Coleoptera					31
573	.1	I	Hymenoptera					31
	.2	I	Hymenoptera					
	.3	I	Thysanoptera					
	.4	I	Diptera: Brachycera: Eremoneura: Cyclorrhapha	Phoridae	*Euliphora*			
574		I	Coleoptera					
575		**I**	**Coleoptera: Polyphaga: Cucujiformia: Cleroidea**	**Cleridae**			**F**	
576		I	Coleoptera: Polyphaga: Cucujiformia: Curculionoidea					

577		I	Coleoptera					32
578		I	Hymenoptera: Evanioidea	Evaniidae				32
579	.1	I	Hymenoptera					32
	.2	I	Hymenoptera: Platygastroidea	Platygastridae				
	.3	I	Hymenoptera: Platygastroidea	Platygastridae				
580		I	Coleoptera					33
581		I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				33
582		A	Acari: Acariformes: Oribatida	Neoliodidae	*Platyliodes?*			34
583		I	Coleoptera					34
584		I	Hymenoptera: Platygastroidea	Platygastridae				34
585		I	Coleoptera: Polyphaga: Elateriformia: Elateroidea					35
586	.1	I	Psocodea: Psocoptera					35
	.2	I	Psocodea: Psocoptera					
587	.1	I	Coleoptera					35
	.2	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae	*Archiaustroconops*			
588	.1	I	Diptera: Brachycera: Tabanomorpha	Rhagionidae				35
	.2	I	Hymenoptera					
	.3	A	Araneae					
589		I	Coleoptera					36
590	.1	I	Raphidioptera	Mesoraphidiidae				36
	.2	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
591		I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				36
592		I	Hymenoptera					36
593		I	Thysanoptera					36
594	.1	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				36
	.2	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
595	.1	I	Raphidioptera	Mesoraphidiidae				36
	.2	I	Diptera: Brachycera: Eremoneura: Empidoidea	Dolichopodidae: Microphorinae?				
596		I	Diptera: "Nematocera": Culicomorpha	Chironomidae				36
597	.1	I	Raphidioptera	Mesoraphidiidae				36

	.2	I	Raphidioptera	Mesoraphidiidae				
	.3	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
	.4	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
	.5	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
	.6	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
	.7	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
	.8	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae				
	.9	I	Indet.					
	.10	I	Hymenoptera					
598	.1	A	Acari: Acariformes: Trombidiformes	Erythraeidae				37
	.2	A	Acari					
	.3	A	Acari					
599		A	Araneae					37
600	.1	I	Coleoptera					
	.2	I	Hymenoptera					
	.3	I	Hymenoptera: Platygastroidea	Platygastridae				
	.4	I	Hymenoptera: Platygastroidea	Platygastridae				
	.5	I	Diptera: Brachycera					
601		I	Coleoptera					
602		I	Coleoptera					
603	.1	I	Hymenoptera: Evanioidea	Evaniidae				30
	.2	I	Hymenoptera					
	.3	I	Hymenoptera					
	.4	I	Hymenoptera					
	.5	I	Hymenoptera					
	.6	I	Hymenoptera					
	.7	I	Diptera: "Nematocera": Culicomorpha	Ceratopogonidae	*Protoculicoides*			
604		I	Diptera: "Nematocera": Culicomorpha	Chironomidae				30
605	.1	I	Hymenoptera					37
	.2	I	Hymenoptera					
	.3	I	Hymenoptera					
	.4	I	Hymenoptera					
	.5	I	Hymenoptera					
	.6	I	Hymenoptera					

	.7	I	Hymenoptera					
	.8	I	Hymenoptera					
	.9	I	Hymenoptera					
	.10	I	Hymenoptera					
	.11	I	Hymenoptera					
	.12	I	Hymenoptera					
	.13	I	Hymenoptera					

ES-07-06	**I**	**Raphidioptera**	**Mesoraphidiidae**	***Cantabroraphidia***	***C. marcanoi***	**H**	
ES-07-07	I	Diptera: "Nematocera": Psychodoidea?					
ES-07-09	**I**	**Diptera: "Nematocera": Culicomorpha**	**Ceratopogonidae**	***Lebanoculicoides***	***L. excantabris***	**H**	
ES-07-17	**I**	**Diptera: "Nematocera": Culicomorpha**	**Ceratopogonidae**	***Archiaustroconops***	***A. borkenti***	**H**	
ES-07-18	**I**	**Diptera: "Nematocera": Culicomorpha**	**Ceratopogonidae**	***Protoculicoides***	***P. skalskii***	**F**	

ANEXO III. Material estudiado relacionado con el presente Proyecto de Tesis Doctoral (material publicado y por publicar)

II.2.1 MATERIAL PUBLICADO (O EN PRENSA). En negrita, los nuevos taxones

II.2.1.1 Material de El Soplao estudiado con motivo del presente Proyecto de Tesis Doctoral

RAPHIDIOPTERA - Pérez-de la Fuente et al. (2010) y Pérez-de la Fuente et al. (2012a): anexo I.3 y anexo I.6

†Mesoraphidiidae

• ***†Cantabroraphidia*** Pérez-de la Fuente, Nel, Peñalver & Delclòs, 2010. Especie tipo: ***C. marcanoi*** Pérez-de la Fuente, Nel, Peñalver & Delclòs, 2010 (ES-07-06).

• ***†Necroraphidia*** Pérez-de la Fuente, Nel, Peñalver & Delclòs, 2010. Especie tipo: ***N. arcuata*** Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012 (CES 391.1).

• ***†Amarantoraphidia*** Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012. Especie tipo: ***A. ventolina*** Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012 (CES 364.1).

• †Mesoraphidiidae indet. (CES 376)

NEUROPTERA

Chrysopoidea - Pérez-de la Fuente et al. (2012e, *reenviado a la revista tras informe favorable de revisores*): anexo I.11

• **Nuevo género y especie** (CES 418)

HYMENOPTERA

Megalyridae - Pérez-de la Fuente et al. (2012b): anexo I.7

• *Megalava truncata* Perrichot, 2009 (CES 391.2).

Evaniidae - Pérez-de la Fuente et al. (2012c): anexo I.8

• ***Cretevania soplaensis*** Pérez-de la Fuente, Peñalver & Ortega-Blanco, 2012 (CES 364.2).

DIPTERA

Ceratopogonidae - Pérez-de la Fuente et al. (2011): anexo I.5

• ***Lebanoculicoides excantabris*** Pérez-de la Fuente, Delclòs, Peñalver & Arillo, 2011 (ES-07-9).

• *Protoculicoides skalskii* Szadziewski & Arillo, 1998 (ES-07-18).

• ***Archiaustroconops borkenti*** Pérez-de la Fuente, Delclòs, Peñalver & Arillo, 2011 (ES-07-17).

• ***Atriculicoides szadziewskii*** Pérez-de la Fuente, Delclòs, Peñalver & Arillo, 2011 (CES 363).

• *Austroconops* sp. (CES 008 y CES 017.1).

ARANEAE

†Lagonomegopidae - Pérez-de la Fuente et al. (2012d, *en prensa*): anexo I.10

• ***†Soplaogonomegops*** Pérez-de la Fuente, Saupe & Selden, 2012. Especie tipo: ***S. unzuei*** Pérez-de la Fuente, Saupe & Selden, 2012 (CES 362).

Oonopidae - Saupe et al. (2012): anexo I.9

• ***Orchestina rabagensis*** Saupe, Pérez-de la Fuente, Selden, Delclòs, Tafforeau & Soriano, 2012 (CES 013).

II.2.1.2. Material de El Soplao estudiado por otros autores

THYSANOPTERA: Thripidae

• ***†Tethysthrips*** Nel, Peñalver, Azar, Hodebert & Nel, 2010. Especie tipo: ***T. hispanicus*** Nel, Peñalver, Azar, Hodebert & Nel, 2010 (CES 451). (Nel et al., 2010)

HYMENOPTERA

†Serphitidae

• ***Microserphites soplaensis*** Ortega-Blanco, Delclòs, Peñalver & Engel, 2011 (CES 566.1) (Ortega-Blanco et al., 2011a)

Mymarommatidae

• ***Archaeromma hispanicum*** Ortega-Blanco, Peñalver, Delclòs & Engel. Alotipo. (CES 452). Holotipo en ámbar de Peñacerrada I. (Ortega-Blanco et al., 2011b)

II.2.1.3. Material de otros ámbares coetáneos al de El Soplao estudiado en el presente Proyecto de Tesis Doctoral

Sigla MCNA. Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz), ámbar de Peñacerrada I (España)

Sigla CPT. Colección Paleontológica de Teruel-Dinópolis (Teruel), ámbar de San Just (España)

Sigla IGR.ARC. Université de Rennes 1, Géosciences (Rennes, Francia), ámbar de Archingeay-Les Nouillers (Francia)

RAPHIDIOPTERA - Pérez-de la Fuente et al. (2012a): anexo I.6

†Baissopteridae

• ***Baissoptera*? *cretaceoelectra*** Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012 (MCNA 12068.4)

†Mesoraphidiidae

• ***Styporaphidia*? *hispanica*** Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012 (MCNA 9343)

• ***†Alavaraphidia*** Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012. Especie tipo: ***A. imperterrita*** Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012 (MCNA 13608)

• Dos †Mesoraphidiidae indet. (MCNA 9218, 9316)

ARANEAE

†Lagonomegopidae - Pérez-de la Fuente et al. (2012d, *en prensa*): anexo I.11

• ***Lagonomegops? cor*** Pérez-de la Fuente, Saupe & Selden, 2012 (MCNA 13295)

• ***†Spinomegops*** Pérez-de la Fuente, Saupe & Selden, 2012. Especie tipo: ***S. arcanus*** Pérez-de la Fuente, Saupe & Selden, 2012 (MCNA 13307). Otras especies incluidas: ***S. aragonensis*** Pérez-de la Fuente, Saupe & Selden, 2012 (CPT 4155)

Oonopidae - Saupe et al. (2012): anexo I.9

• ***Orchestina gappi*** Saupe, Pérez-de la Fuente, Selden, Delclòs, Tafforeau & Soriano, 2012 (IGR.ARC-28.2)

• *Orchestina* sp. (MCNA 12593)

• *Orchestina* sp. (CPT 4100)

II.2.2. MATERIAL POR PUBLICAR

El material listado a continuación se halla en diversas fases de estudio dentro del presente Proyecto de Tesis Doctoral y será publicado en diferentes trabajos. El trabajo realizado referente a arañas palpimanoideas se amplía en el anexo IV, mientras que el de neurópteros se amplía en el anexo V.

II.2.2.1. Material de El Soplao estudiado con motivo del presente Proyecto de Tesis Doctoral

NEUROPTERA

Berothidae (anexo V)

• Nuevo género 1 y especie 1 (CES 004)

• Nueva especie 2 perteneciente al género *Ethiroberotha*? (CES 014)

Coniopterygidae (anexo V)

• Nueva especie perteneciente al género †*Glaesoconis.* Basada en varios ejemplares (ejemplar seleccionado para constituir el futuro holotipo CES 348)

Psychopsidae (anexo V)

• Nuevo género y especie (CES 390.1)

DIPTERA

†Zhangsolvidae

• Nuevo género y especie. Basado en holotipo hembra (CES 015.2 + 392.2), paratipo macho (0.15.3 + 392.3), y alotipo hembra (CES 349.1).

II.2.2.2. Material de otros ámbares coetáneos al de El Soplao estudiado con motivo del presente Proyecto de Tesis Doctoral

NEUROPTERA

Berothidae (anexo V)

• Nuevo género 2 con dos nuevas especies, especie 3 y especie 4 (MCNA 8644.1 y MCNA 9728)

• Nuevo género 3 y especie 5 (CPT 4144)

• Larva de berótido (MCNA 9294)

• Cuatro Berothidae indet. (MCNA 9902, 10033, 12590 y 13379)

ARANEAE

Palpimanoidea (anexo IV)

• Nuevo género 1 y especie 1 basada en tres ejemplares (MCNA 12570, 12571 y 12580)

• Nuevo género 2 y especie 2 basada en un ejemplar (MCNA 9931)

• Nueva especie 3 (MCNA 9760)

ANEXO VI: Resumen en inglés/English summary

VI.1. Main objective and methods

This PhD dissertation aimed to achieve in-depth knowledge of the paleobiology associated with the arthropods from the El Soplao amber outcrop (Rábago, Cantabria, Northern Spain), allowing for a preliminary comparison with primary Cretaceous amber outcrops. This was possible only after a thorough systematic treatment of El Soplao arthropod inclusions that inferred their paleoautoecological, paleobiogeographical and paleoethological contexts to, ultimately, glean a holistic understanding of the paleoenvironmental setting.

The discovery of El Soplao outcrop took place in 2007. Four amber excavations occurred in October of 2008, March and July of 2009, and March of 2010. Searches for bioinclusions, specimen preparation, and creating/updating the El Soplao inclusion database was carried out by the geologist and gemologist Mr. Rafael López del Valle, expert in amber preparation. All the studied material is currently housed at the laboratory of the institutional collection from the El Soplao outcrop in El Soplao cave (Celis, Cantabria). The collection, named CES ("Colección El Soplao"; appendix II), is composed of amber pieces with bioinclusions, amber pieces with particular taphonomic interest, and paleontological material associated with the amber. Each preparation received its own CES registry number. Syninclusions within the same preparation have the same CES registry number but have a unique number, e.g. CES 530.7 (preparation 530, inclusion number 7). Moreover, several preparations may come from the same original amber piece, in which case they have the same syninclusion reference (= RS). Therefore, all the inclusions within preparations sharing an RS are syninclusions. The registry number ES-07-xx was given to the first material from El Soplao available for study. It was temporarily housed in the "Museo Geominero", from the "Instituto Geológico y Minero de España" (IGME), in Madrid, as the final destination of these material was the CES collection in Cantabria. Although some holotypes still lack a CES number (with only an ES-07-xx number), they will exclusively have a CES number in the future.

The geology of the El Soplao outcrop and the paleontological material associated with the amber pieces were studied in detail by Najarro et al., 2009, 2010 (see appendices I.1 and I.2), who concluded an Early Albian age for the deposit. Geological context of the Spanish ambers can be found in Peñalver & Delclòs (2010). An overwiew of amber taphonomy is provided by Martínez-Delclòs et al. (2004).

Arthropod groups of particular novelty and those discovered in other Spanish ambers were given priority for study, namely insects and spiders. Studied insect orders included Raphidioptera, Neuroptera, Hymenoptera and Diptera. Raphidioptera and Neuroptera had not been formerly described from Spanish amber, and studied spiders were few (Penney, 2006a; Penney & Ortuño, 2006). Study of El Soplao bioinclusions was often conducted together with available samples from other Albian localities, i.e., the Spanish ambers of Peñacerrada I (= Moraza, belonging to the so-called Álava amber) and San Just (Teruel), and the French amber from Archingeay-Les Nouillers. Determination of unpublished El Soplao amber specimens was

performed in collaboration with by the following colleagues: Mr. David Cerdán (Universitat de Barcelona) for coleopterans; Dr. Jaime Ortega-Blanco and Dr. Michael Engel (University of Kansas) for hymenopterans; and Dr. Antonio Arillo (Universidad Complutense de Madrid) for brachyceran dipterans and mites. The published papers (or in other editorial stages) are included in appendix I. Two unpublished studies are presented in appendices IV and V. The first study is a phylogenetic analysis of the spider superfamily Palpimanoidea using both extinct and extant taxa (including three new morphotypes from Spanish amber, the classification of which were problematic). The second unpublished study is an assessment of the diversity of neuropterans in Spanish amber (apart from the new chrysopoid neuropteran larva, see Pérez-de la Fuente et al., 2012e, *resent to the journal after referees' favorable report*: appendix I.11).

VI.2. Results

A total of 549 arthropod inclusions from El Soplao amber have been determined and catalogued. The inclusions correspond to 13 hexapod orders (with about 40 determined families), four arachnid orders (spiders and three orders of mites) and one crustacean order (Fig. 22). Hymenopterans are the most abundant arthropods (41.9% of total bioinclusions), followed by dipterans (23.3%) and coleopterans (9.2%). These three groups represent 74.5% of total arthropod bioinclusions found in El Soplao. The remaining arthropod groups are minor in terms of relative abundance, as each of them represents less than 5% of total arthropod bioinclusions. These groups are (in order of abundance): thysanopterans, psocodeans, hemipterans, spiders, mites, neuropterans, raphidiopterans, blattids, lepidopterans, collembolans, isopterans, mecopterans and tanaid crustaceans. The list of recovered specimens classified at familiar level (or superfamiliar level) for each arthropod group is shown in Table 3. The different arthropod groups that have been recognized so far from El Soplao amber are illustrated in section 6. A detailed list of all catalogued samples to date (July 2012) is shown in appendix II. A summary of the studied material related with the present PhD dissertation (both published or to be published) is presented in appendix III. Non-arthropod inclusions found in El Soplao amber include microbioinclusions like fungi, plant remains like fusinite fibers and trichomes, and some vertebrate remains, i.e. feathers (belonging to non-avian theropods or primitive birds) and reptile skin fragments (section 6.4).

The following publications have resulted from the study of El Soplao amber arthropods and are included within the present dissertation: Pérez-de la Fuente et al. (2010, 2012a: appendices I.3 and I.6) (Raphidiopterans); Pérez-de la Fuente et al. (2012e, *resent to the journal after referees' favorable report*: appendix I.11; see also appendix V) (Neuropterans); Pérez-de la Fuente et al. (2012b,c: appendices I.7 and I.8) (Hymenopterans); Pérez-de la Fuente et al. (2011: appendix I.5) (Dipterans); and Saupe et al. (2012: appendix I.9) and Pérez-de la Fuente et al. (2012d, *in press*: appendix I.10); see also appendix IV) (Spiders). In addition, synchrotron X-ray imaging has been employed for study of some samples, demonstrating the potential of this technique in elucidating paleobiological data (Soriano et al., 2010: appendix I.4; Saupe et al., 2012: appendix I.9; see also appendix IV). Colleagues belonging to our

research team carried out other studies on El Soplao inclusions, including thysanopteran and hymenopteran samples from El Soplao (Nel et al., 2010; Ortega-Blanco et al., 2011a,b).

VI.3. Discussion

VI.3.1. Taphonomy and paleoenvironmental reconstruction

The paleobiological data gathered from El Soplao amber and its bioinclusions during the course of this PhD dissertation complements the taphonomic and the paleoenvironmental data provided by geology and paleontological material associated with the amber (see Najarro et al., 2009: appendix I.1).

An abundance of fragile amber pieces occur in the El Soplao outcrop (Fig. 20), with these pieces being unlikely to have withstood intense or prolonged transport. Furthermore, branched shoots of †*Frenelopsis sp.* (Fig. 19A; Najarro et al., 2010: appendix I.2), roots *in situ* (Fig. 19B) and rhizocretions (Fig. 19C) are found with the amber. These indicators suggest the resin traveled little after secretion and before burial. As such, the resin and eventually amber deposit is considered para-autochtonous in origin.

Paleofires may have promoted the secretion and posterior accumulation of resin leading to the formation of the El Soplao amber deposit. Three lines of evidence support the presence of fires. The first and most sound piece of evidence is the abundance of fusainized plant matter associated with the amber and the existence of fusainized plant fibers as inclusions in the amber (section 6.4.2; Najarro et al., 2010: appendix I.2; Pérez-de la Fuente et al., 2012a,b: appendices I.6 and I.7). The second piece of evidence is the particular abundance of raphidiopterans (mesoraphidiids), which could be explained by the mass of available wood after fires (Pérez-de la Fuente et al., 2012a: appendix I.6). Lastly, the new chrysopoid neuropteran larva morphotype was carrying a trash-packet made of fern trichomes with affinity to the family Gleicheniaceae. This fern family indicates the presence of paleofires, as these ferns are primary colonizers after fires or lava flows since, at least, the Late Jurassic (Pérez-de la Fuente et al., 2012e, *resent to the journal after referees' favorable report*: appendix I.11). Insects with wood-boring habits, like beetles of the superfamily Curculionoidea (section A.9.2.4; Najarro et al., 2010: appendix I.2), may also have promoted resin secretion.

The bioinclusions within El Soplao amber indicate the secreted resin was highly fluid. The most representative example is provided by the intricate cloud of trichomes that form the trash-packet on the chrysopoid neuropteran larva (Pérez-de la Fuente et al., 2012e, *resent to the journal after referees' favorable report*: appendix I.11). This structure could have not been included in the resin homogeneously sans bubble formation without a low-viscosity, fluid resin at the time of inclusion.

The presence of the ceratopogonid genus *Austroconops* (Pérez-de la Fuente et al., 2011: appendix I.5), the dolichopodid genus †*Cretomicrophorus* (section A.12.2.3.1.3) and a tanaid crustacean (section 6.3.3) in El Soplao amber suggests that the plant sources responsible for resin secretion were located close to the coastline. Other evidence, after

recognition of the para-autochtony of the deposit, are fossils of marine or brackish mollusks associated with the amber (section 4.2.3) and amber pieces colonized by bryozoans and/or serpulids (Najarro et al., 2010: appendix I.2). The latter indicate how the resin pieces were exposed to brackish or marine waters for relatively long periods before burial.

VI.3.2. Paleofaunistic comparison

The El Soplao arthropod paleodiversity was compared to that of other prominent Cretaceous amber deposits (see bold entries in Table 1). These data, however, must be interpreted cautiously, as the number of available inclusions is limited.

Hymenopterans are the most abundant arthropods in El Soplao. This contrasts with the majority of main Cretaceous ambers, in which dipterans are the most abundant arthropods (Table 4). Proctotrupomorphan wasps represent the most abundant hymenopteran lineage in all Cretaceous ambers, and this is not an exception in El Soplao. Their small size and low ability to fly explain the presence-bias of their record (section 5; Martínez-Delclòs et al., 2004). Platygastrids (section A.10.1.3.2) are the most prevalent hymenopterans, corresponding to 40.4% of total hymenopterans and 16.9% of total macrobioinclusions from El Soplao. Such an abundance of platygastrids, although to a lesser extent, is found in other Cretaceous ambers (Ortega-Blanco, 2010; McKellar & Engel, 2012). Other proctotrupomorphan wasps, like serphitids and mymarommatids (section A.10.1.3.1) are as abundant as in other Cretaceous ambers (Ortega-Blanco et al., 2011a,b; Engel et al., 2011). The total absence of ants in El Soplao amber (and Spanish amber in general), which are present in ambers from Myanmar and France, is remarkable. Apart from taphonomic reasons, the absence of ants could be explained because of a relatively rapid diversification of the clade in the Late Albian or because they were absent from the Iberian Plate during the Albian due to its isolation from the rest of Laurasia. On the contrary, the proctotrupomorphan family †Stigmaphronidae is absent from French amber but is diverse in Spanish amber, especially in Peñacerrada I, and has been also recorded from El Soplao (section A.10.1.3.3). Furthermore, the description of a new species belonging to the evaniid genus †*Cretevania* from El Soplao further increases the high diversity of this genus in Spanish amber (Pérez-de la Fuente et al., 2012c: appendix I.8).

Relative abundance of nematoceran and brachyceran dipterans is similar, although the former are somewhat more abundant. Ceratopogonids (biting midges) represent one-third of total dipterans (and the most abundant dipteran group) as well as 7.8% of total macrobioinclusion diversity (i.e., the second most abundant arthropod group after platygastrid wasps). A prevalence of ceratopogonids also occurs in other Cretaceous ambers, a fact which may be related to the ecological proximity of ceratopogonids to resin sources, their small size, and their swarming behavior (section 5; Martínez-Delclòs et al., 2004). The smaller proportion of dipterans in El Soplao amber could be explained by other nematoceran groups like chironomids, psychodids and cecidomyiids that do not appear in El Soplao as abundant in other Cretaceous ambers. The diversity of brachyceran dipterans is high and the proportions of the different groups are equivalent to those of other Cretaceous ambers, excluding the high abundance of Dolichopodidae from Archingeay-Les Nouillers amber (representing about 6% of

total inclusions; Perrichot et al., 2007). This difference could reflect a greater marine influence on the area in which the resin secretion took place, as marine microbioinclusions have also been reported from this French amber deposit (Girard et al., 2009).

The abundance of coleopterans in El Soplao amber is relatively high when compared with ambers from Lebanon (Hammana), other Spanish outcrops (Peñacerrada I) and France (Archingeay-Les Nouillers), but not as high as in Myanmar amber (Table 4). Hemipteran abundance, however, is lower in El Soplao than in the main Cretaceous ambers (Table 4; see also Grimaldi & Nascimbene, 2010), which is likely due to the low proportion of coccoids, common in ambers from Lebanon, other Spanish outcrops (Peñacerrada I), Myanmar and USA (New Jersey) (Azar, 2000; Grimaldi et al., 2002; Delclòs et al., 2007; Grimaldi & Nascimbene, 2010). In Russian (Taimyr) and Canadian ambers, the main sternorrhynchan hemipterans are aphidoids, which likely reflects that this group was better adapted to a more seasonal paleoclimate (Grimaldi & Engel, 2005)

El Soplao amber has a high relative abundance of raphidiopterans (Table 4; Pérez-de la Fuente et al., 2012a: appendix I.6). There are, at least, ten times more raphidiopterans in El Soplao amber than in any other known Cretaceous amber. Their unusual abundance could be an indication of paleofires. Fires would have increased the availability of dead wood as a substrate for the xylophagous or xylophilous insects to develop, which, in turn, could have aided the increase in the xylophilous, predatory snakefly populations. Likewise, although to a lesser extent than raphidiopterans, neuropterans also seem to be especially abundant and diverse in El Soplao (Table 4; appendix V).

The presence of a representative of the order Mecoptera (section A.11) is extremely rare, as no records of this order from other Cretaceous ambers are known with the exception of two specimens from Burmese amber (Grimaldi et al., 2005), despite that some ambers, like Lebanese amber, have provided thousands of bioinclusions (Azar et al., 2010a). Other inclusions are even more exceptional, as they were completely unknown from Cretaceous ambers, and include the new morphotype belonging to the neuropteran family Psychopsidae (appendix V), the new larval morphotype belonging to the neuropteran superfamily Chrysopoidea (Pérez-de la Fuente et al., 2012e, *resent to the journal after referees' favorable report*: appendix I.11), and three specimens preserved as syninclusions representing a new morphotype belonging to the dipteran family †Zhangsolvidae (section A.12.2.1).

The diversity of arachnids in El Soplao amber is remarkable. The oldest oonopid spider found to date was described (Saupe et al., 2012: appendix I.9) along with one spider belonging to the family †Lagonomegopidae (Pérez-de la Fuente et al., 2012d, *in press*: appendix I.10). The latter specimen indicated this enigmatic Cretaceous spider family could have affinities with the superfamily Palpimanoidea, which has a relatively good record in Spanish amber (appendix IV). Spider webs are also abundant in El Soplao amber. Samples with particular paleoecological interest are known, as they have trapped prey and even the potential weaving spider as syninclusions (section B.1.3). Furthermore, El Soplao amber has provided the oldest known record for several mite groups, i.e. the trombidiform family Bdellidae (section B.2.1.1.2), the oribatid families Neoliodidae and Nothridae (sections B.2.1.2.1 and B.2.1.2.2), and, more

remarkably, the oldest known record of the whole superorder Parasitiformes, with a specimen belonging to the family Argasidae (section B.2.2).

Several arthropod groups present in other, prominent Cretaceous ambers have not appeared in El Soplao (Table 4). However, when present, their proportion is so low in other outcrops that their absence in El Soplao could be a statistical artifact. The absence of orthopterans (crickets and grasshoppers), which are relatively abundant in French amber from Archingeay-Les Nouillers (3% of total inclusions) (Table 4), is noteworthy. The abundance of orthopterans in this French outcrop has been suggested to reflect a high proportion of amber pieces that preserved edaphic fauna (Perrichot, 2004). Then, their absence from El Soplao could indicate the low amount of resin that would have reached the soil, which is in keep with the large number of aerial amber pieces observed in the El Soplao outcrop (Najarro et al., 2009: appendix I.1).

The three insect species formally described from both El Soplao and Peñacerrada I ambers are two hymenopterans and one dipteran: the megalyrid *Megalava truncata* (Perrichot, 2009; Pérez-de la Fuente et al., 2012b: appendix I.7), the mymarommatid *Archaeromma hispanicum* (Ortega-Blanco et al., 2011b) and the ceratopogonid *Protoculicoides skalskii* (Szadziewski & Arillo, 1998; Pérez-de la Fuente et al., 2011: appendix I.5). The latter was also found in the Spanish amber outcrop of San Just (Arillo et al., 2008b). A fourth species that occurs both in El Soplao and Peñacerrada I (a platygastrid wasp) has not been formally described yet (Ortega-Blanco, 2010). Correlation of outcrops using paleoentomological data was performed by McKellar et al. (2008) for the ambers from Canada and by Azar et al. (2010a) for the ambers from Lebanon. Altogether, the shared species between the El Soplao and Peñacerrada I ambers represent paleoentomological evidence that supports the geological data and the remaining paleobiological data that indicate a similar age for these Basque-Cantabrian Basin amber outcrops. Geological and paleobotanical data also indicate, however, paleoenvironmental differences between the amber outcrops, with a higher marine influence for the El Soplao outcrop than for the Peñacerrada I outcrop (Peñalver & Delclòs, 2010).

The paleofaunas from El Soplao and Lebanese ambers show similarities. Two new species belonging to genera also described from Lebanese amber, but unknown from any other Cretaceous amber, have been described from El Soplao. The first is the ceratopogonid *Lebanoculicoides excantabris.* The genus †*Lebanoculicoides* was formerly described from Lebanese amber (Szadziewski, 1996) and represents the most ancestral lineage of the family Ceratopogonidae (section I.5; Pérez-de la Fuente et al., 2011). The second species is the thysanopteran *Tethysthrips hispanicus* (Nel et al., 2010). This species highly resembles the other species of this genus, *T. libanicus*, from Lebanese amber (ibid.). In addition, exclusive faunistic similarities between the ambers from Lebanon and Peñacerrada I can be found. This is the case for the stigmaphronid wasp genus †*Libanophron* Ortega-Blanco, Delclòs & Engel, 2011, which is known from one Lebanese species (Engel & Grimaldi, 2009) and a Spanish one described from Peñacerrada I amber (Ortega-Blanco et al., 2011).

VI.3.3. Paleobiotic interactions - Paleoethology

The study of syninclusions has the potential to reflect con-specificity and sexual dimorphisms, and/or to provide information about paleobiotic interactions between organisms preserved in amber. Syninclusions are common in El Soplao amber (Fig. 7; Najarro et al., 2009: fig. 12D, appendix I.1). Only 14% of total bioinclusions from El Soplao (79 of the 549) are preserved isolated, i.e. without any syninclusions. Ten of the amber pieces originally contained more than ten syninclusions. The highest number of syninclusions in El Soplao is 52, although the original piece containing these syninclusions was subdivided into several preparations (appendix II).

El Soplao amber has provided evidence of paleobiotic interactions, often preserving direct evidence of paleoethology. Two intraspecific paleobiotic interactions are known and occur in dipterans. First, possible instances of swarming due to gregarious behavior, which are common in some dipteran groups, have been found. Seven specimens belonging to the genus †*Euliphora* (Phoridae) were originally discovered in the same amber piece but posteriorly subdivided in five different preparations (section A.12.2.3.3). Previously reported instances of swarming in phorid flies are known from Canadian amber (Brown & Pike, 1990). Another possible case of swarming corresponds to the new morphotype of undetermined brachyceran dipteran (new species A, appendix II), with five specimens originally found as syninclusions. Furthermore, two ceratoponid dipterans assigned to the genus †*Lebanoculicoides* (CES 423.1 + 423.2) have been found in mating position (section A.12.1.1.1). Although finding two arthropods mating in amber is exceptional, there are several records known from Cenozoic ambers from the Baltic and Dominican Republic (see Arillo, 2007). However, the only other Cretaceous record comparable to that of El Soplao is two mating dipterans from the family Scatopsidae in Lebanese amber (Azar et al., 2010a).

Four samples reflecting interspecific paleobiotic interactions are known from El Soplao amber. The first instance is the new morphotype of chrysopoid neuropteran larva and its trash-packet gathered from trichomes with affinities to gleicheniacean ferns (Pérez-de la Fuente et al., 2012e, *resent to the journal after referees' favorable report*: appendix I.11). This inclusion represents an ancient plant-insect interaction and the oldest known evidence of trash-carrying behavior, which provides camouflage and physical protection against predators and prey. The second example of interspecific interaction is a chironomid dipteran that was ectoparasitized by an undetermined mite (CES 531.1 + 531.2) (section A.12.1.1.2). Mites are the most common ectoparasites in amber (Arillo, 2007). The third instance of interspecific paleobiotic interaction corresponds to arthropod groups that would have had hematophagous habits, presumably feeding from vertebrate blood, i.e., the ceratopogonid dipterans (Pérez-de la Fuente et al., 2011: appendix I.5), the phlebotomid dipterans (section A.12.1.2) and the specimen belonging to the family Argasidae, or "soft ticks" (section B.2.2). An additional group in which hematophagy is known is the dipteran family Rhagionidae (section A.12.2.2). The last case of interspecific paleobiotic interactions in El Soplao is provided by one sample in which a complex spider web is preserved together with several trapped prey items and the possible weaving spider, reflecting a possible predator-prey relationship (section B.1.3).

VI. 4. Conclusions

The resin-producing plants responsible for El Soplao amber are conifers belonging to the extinct family Cheirolepidiaceae and, at least, another unknown conifer group. These trees would have lived close to the paleo-coastline. Paleofires played a leading role in the production and accumulation of resin by promoting traumatic secretion of resin (in which wood-boring insects could have contributed) and by removing plant coverage on the forest floor. Removal of vegetation promoted soil erosion by water run-off and the mobilization of deposited resin. The resin was transported only a short distance before deposition in para-autochtonous areas, where final burial took place (there is no evidence of reworking of the amber pieces). The areas where the resin was buried and fossilized correspond to marshy or delta-estuarine environments. Some resin pieces had a long exposure time to marine or brackish waters before being buried.

In spite of the infant stage of study of El Soplao amber, identified arthropod diversity is high, and the outcrop has provided the oldest known records for certain taxa. Thirteen hexapod orders (composed by about 40 families), four arachnid orders, and one crustacean order have been determined from 549 catalogued arthropod inclusions. The arthropod fauna from El Soplao is quantitatively and qualitatively singular when compared to faunas from other known Cretaceous ambers.

Quantitatively, and cautiously as these analyses would greatly benefit from discovery of additional specimens, the relative abundances of hymenopterans, raphidiopterans and, to a lesser extent, neuropterans, in El Soplao amber are the highest among Cretaceous ambers of similar age. On the contrary, the relative abundances of dipterans and hemipterans are the lowest. Until now, there has been no record of orthopterans in El Soplao amber. This absence could indicate that the resin did not reach the forest floor and therefore did not trap edaphic fauna, which would be in-line with the abundance of aerial amber pieces present in the El Soplao outcrop.

From a qualitative point of view, some findings from El Soplao amber are exceptional due to their scarcity in the Cretaceous amber fossil record. Such is the case for new morphotypes from four insect groups: the psychopsid neuropteran based on a complete specimen, the chrysopoid neuropteran larva preserved together with its trash-packet, the three zhangsolvid dipterans preserved as syninclusions, and, lastly, the mecopteran specimen.

The faunistic singularities in El Soplao amber, both from the quantitative and qualitative point of view, apart from taphonomic causes, could reflect the endemic nature of the Albian Iberian ecosystems due to the insularity that the Iberian Plate achieved during the Lower Jurassic.

Three insect species occur in both the El Soplao and Peñacerrada I (=Moraza) outcrops. The shared species between these two Basque-Cantabrian Basin outcrops suggest they are similar in age. Moreover, similarities have been noted between the paleofauna from the Spanish amber outcrops (El Soplao and Peñacerrada I) (Albian) and the paleofauna from Lebanon (Barremian-Aptian), despite these outcrops are separated in time by several million years. It is necessary, however, to increase the Spanish amber collections in order to provide

more support for these observations, and to revise the age dating for the Lebanese amber outcrops.

El Soplao amber is valuable in the abundance of syninclusions and samples that provide information about paleoethology and paleobiotic interactions. There are instances of possible swarming, mating, camouflage/defense, plant-insect relationship, parasitism, possible hematophagy and possible predator-prey relationship.

In conclusion, El Soplao amber provides a unique window in which to understand the terrestrial Iberian ecosystems in the Cretaceous.